

THESIS

IMPROVING UNGULATE HABITAT IN A REGION UNDERGOING RAPID ENERGY
DEVELOPMENT: CONSEQUENCES FOR SONGBIRDS AND SMALL MAMMALS

Submitted by

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ABSTRACT

IMPROVING UNGULATE HABITAT IN A REGION UNDERGOING RAPID ENERGY DEVELOPMENT: CONSEQUENCES FOR SONGBIRDS AND SMALL MAMMALS

Habitat manipulation intended to mitigate the impact of energy development on game animals is well underway in the western U.S. Yet, the consequences of these actions for other species are not well understood. A habitat manipulation experiment was established in the Piceance Basin, a region of Colorado undergoing rapid energy development, to evaluate alternative methods (i.e. chaining, hydro-axe, and roller-chop treatments) for reducing pinyon-juniper woodlands to promote mule deer habitat. I use this experimental design to additionally test the initial effects of these treatments on birds and small mammals, and to evaluate selection of habitat components in treatments by birds and small mammals. I found lower bird species occupancy in all treatment plots compared to control plots; however the strength of this response varied by bird guild. I found a positive relationship between bird species occupancy and percent tree cover and a negative relationship between bird species occupancy and percent grass and forb cover. I found no evidence of differences in small mammal species occupancy or density between controls and treatments. I found a positive relationship between small mammal species occupancy and percent grass and forb cover. Species richness did not significantly differ between control and treatment plots for birds or small mammals. My approach and research findings can be used to inform habitat management and multiple-species conservation objectives in pinyon-juniper and sage-steppe ecosystems undergoing energy development. Specifically, I have identified that recently developed roller-chop and hydro-axe treatments have similar

impacts to woodland bird guilds as traditional chaining treatments. I have also identified species that are sensitive to habitat mitigation treatments, and thus should be monitored if woodland reduction continues to be used as a habitat mitigation strategy. Since all bird guilds were positively associated with tree cover, woodland reduction strategies that promote landscape heterogeneity by leaving standing trees to provide structure for birds may have fewer impacts than those that clear large contiguous patches of woodland. This approach has the potential to increase the conservation value of habitat mitigation treatments for pinyon-juniper obligates as well as shrubland and grassland species.

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PREFACE

Recent emphasis on domestic production has generated substantial interest in exploiting energy reserves in the western United States. Crude oil and natural gas production has been increasing in the U.S. and is projected to grow by 20% through at least 2040 (EIA 2012). This growing focus on domestic production in the United States is leading to large-scale land-use changes (Copeland et al. 2011), with important consequences for native plant and animal assemblages (Bartis et al. 2005, Gilbert and Chalfoun 2011, McDonald et al. 2009, Northrup and Wittemyer 2013). These impacts include habitat fragmentation and direct habitat loss, and altered disturbance regimes such as changes in the fire cycle (Forbes et al. 2004, McDonald et al. 2009, Northrup and Wittemyer 2013).

Habitat mitigation is an important approach to addressing and reducing the impacts of energy development on natural communities. The mitigation hierarchy involves a three-step sequence that guides mitigation decisions and progresses from avoidance of impacts, to minimization of adverse impacts, to compensation when adverse impacts are unavoidable (DOD-EPA 2008). Methods of compensatory mitigation include creation of new habitat of comparable quality, enhancement of existing habitat to improve quality, preservation of existing habitat, or restoration of degraded habitat (DOD-EPA 2008). Future development of U.S. energy reserves is likely to warrant widespread compensatory habitat mitigation, especially for desirable game species and species protected under the Endangered Species Act. Yet habitat mitigation is also a form of land use change, and the effects of habitat mitigation on non-targeted wildlife are not well understood, especially in the context of energy development. Habitat mitigation intended to benefit a target species may differentially affect non-targeted species, and nearby energy

exploitation may exacerbate impacts to some non-targeted wildlife populations. Thus, research is needed to understand the consequences of species-specific habitat mitigation for the conservation of multiple species in energy development-impacted landscapes.

My research addresses this knowledge gap by investigating songbird and small mammal responses to experimental mule deer (*Odocoileus hemionus*) habitat mitigation treatments in the Piceance Basin, northwest Colorado. The Piceance Basin is an ideal area to address these objectives. The basin contains reserves of coal, natural gas, and oil shale that have made it the target of intense energy development. Resource extraction is well underway and potentially threatens important wintering grounds for one of the largest mule deer herds in the western U.S. (White & Lubow 2002, Lendrum et al. 2012). Furthermore, this region's grassland and shrubland ecosystems are increasingly subject to pinyon-juniper woodland encroachment (Stevens 1999). Thus, recent habitat mitigation treatments have focused on reducing pinyon-juniper overstory and restoring a shrub, herb and grass community to benefit mule deer and mitigate any negative impacts of energy development. Due to the need for better information on methods that are effective, economically viable and practical for land managers, an experiment was established to test alternative approaches (chaining, roller-chopping, and hydro-axing) to reduce pinyon-juniper overstory and promote mule deer habitat. To maximize the information obtained from this experiment, I additionally test the effects of these methods on population dynamics and habitat selection of the small mammal and songbird community.

In chapter one, I provide an overview of the history of land-use changes associated with woodland reduction in pinyon-juniper ecosystems. I review pinyon-juniper expansion and management history, and pinyon-juniper ecosystem wildlife habitat associations.

In chapter two, I evaluate songbird and small mammal population- and community-level responses to alternative habitat mitigation treatments. I compared occupancy, density and species richness response variables among the alternative treatments and controls. I also determined what habitat components birds and small mammals were selecting within the treatment areas by using occupancy modeling to estimate the probability of occupancy as a function of percent cover of each habitat component.

My approach and research findings can be used to inform habitat management and multiple-species conservation objectives in pinyon-juniper and sage-steppe ecosystems undergoing energy development. Previous research on the effects of pinyon-juniper removal on songbirds and small mammals has been largely restricted to impacts from chaining (O'Meara et al. 1981, Sedgwick and Ryder 1987), the primary method traditionally employed by land managers to reduce pinyon-juniper overstory for livestock and wild ungulate habitat improvement (Short and McCulloch 1977). However, alternative woodland reduction methods are already being implemented, and their use is likely to expand in response to pinyon-juniper encroachment and energy development. My research thus represents the first comparison of the effects of these different habitat mitigation strategies on animal assemblages. Information on the impacts of alternate habitat mitigation methods on species diversity, density, and habitat use will help land managers adopt strategies that maximize benefits to game species as well as songbirds and small mammals.

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CHAPTER ONE

EXPANSION OF PINYON-JUNIPER WOODLANDS AND LAND USE CHANGE IN THE WESTERN U.S.: CONSEQUENCES FOR WILDLIFE

INTRODUCTION

Pinyon-juniper (*Pinus edulis*, *Juniperus* spp.) woodlands are one of the most extensive ecosystems in western North America (West 1984) and support a high diversity of animal species compared with many other plant communities in this region (Paulin et al. 1999). However, pinyon-juniper woodlands have expanded rapidly over the past century (Blackburn and Tueller 1970, Miller and Rose 1995, Miller and Rose 1999, Stevens 1999). Whether or not pinyon-juniper expansion is perceived as negative depends on regional management objectives and is often taxon-dependent (Belsky 1996). Where the effects of this expansion on surrounding sage-steppe and forest ecosystems are of conservation concern (Belsky 1996, Noson et al. 2006), natural resource managers frequently reduce pinyon-juniper overstory to limit its spread (Miller and Wigand 1994).

In addition to pinyon-juniper expansion, western North America is undergoing large-scale land use change from unprecedented energy development (Copeland et al. 2011). Active oil and gas production currently occurs on 25 million ha, and with 59 million ha of active or pending leases, there is significant potential for the rate and extent of land subject to energy extraction to continue to rise (Copeland et al. 2011). Cumulative estimates of the current and future ecological footprint of energy development on western North America range from 20.6 million ha (McDonald et al. 2009) to 96 million ha (Copeland et al. 2011).

Energy development has well-documented impacts on wildlife (Sawyer et al. 2006, Walker et al. 2007, Sawyer et al. 2009, Holloran et al. 2010, Gilbert and Chalfoun 2011, McDonald et al. 2009, Northrup and Wittemyer 2013), which have generated the need for compensatory habitat mitigation to offset these impacts (Northrup and Wittemyer 2013). Methods of compensatory mitigation include creation of new habitat of comparable quality, enhancement of existing habitat to improve quality, preservation of existing habitat, or restoration of degraded habitat (DOD-EPA 2008). Future development of U.S. energy reserves is likely to warrant widespread compensatory habitat mitigation, especially for desirable game species and species protected under the Endangered Species Act. In pinyon-juniper woodlands, habitat mitigation has typically involved mechanical pinyon-juniper removal (henceforth referred to as woodland reduction) to promote a shrub, herb and grass community that supports livestock and wildlife, especially game species (Skousen et al. 1989, Bergman et al. 2014).

Woodland reduction to limit pinyon-juniper expansion or to enhance habitat for target species may not benefit all animal species; pinyon-juniper obligates may decline and the impacts on most other taxa are not well known. With expansion of pinyon-juniper woodlands and a potential increase in the frequency of woodland reduction to offset energy development impacts on game species, there is a clear need to synthesize our current knowledge on pinyon-juniper wildlife habitat associations and the effects of woodland reduction on wildlife. The objectives of this review are to: 1) characterize wildlife habitat associations in pinyon-juniper ecosystems, 2) summarize the history of pinyon-juniper expansion and woodland reduction in western North America, 3) describe wildlife responses to woodland reduction activities, and 4) highlight future research priorities in these ecosystems. I draw on the results of the review to discuss how my

findings can be used to inform woodland reduction strategies that achieve multi-species conservation objectives.

Wildlife in Pinyon-Juniper Communities

Pinyon-juniper woodlands support a large assemblage of wildlife species. Finch and Ruggiero (1993) indicated that 107 birds and 62 mammals occur in the pinyon-juniper ecosystem. At least 73 bird species breed in pinyon-juniper woodlands, of which approximately 30 are thought to breed regularly in this ecosystem (Balda and Masters 1980). Over half of these breeding birds are neotropical migrants (Balda and Masters 1980), and pinyon-juniper woodlands may provide essential breeding habitat for several of these species, especially blue-gray gnatcatchers (*Polioptila caerulea*), black-throated gray warblers (*Setophaga nigrescens*) and gray flycatchers (*Empidonax wrightii*) (Webb 1999). Paulin et al. (1999) found that pinyon-juniper woodlands in Utah had more obligate and semi-obligate bird species than any other forest habitat type, except riparian woodlands. They also found higher abundance of all birds in pinyon-juniper woodlands than in all other western habitats with the exception of aspen and riparian woodlands. In addition, pinyon-juniper woodlands have the fourth highest species richness and diversity values relative to other forest types (Paulin et al. 1999). For these reasons, Paulin et al. (1999) contended that pinyon-juniper woodlands are very important for maintaining bird diversity at landscape scales.

Pinyon-juniper habitat supports bird diversity year-round (Sieg 1991). In comparison to surrounding grassland habitats, pinyon-juniper stands maintained a larger number of species and over double the number of individuals consistently through every season; additionally, twice as many species were found nesting in pinyon-juniper during the breeding season (Sieg 1991). Sieg (1991) was keen to point out that spring bird surveys underestimate the year-long value of

pinyon-juniper habitat for thermal cover and food resources for overwintering birds, corridors for migrating birds, and summer perching and nesting sites. However, Balda and Masters (1980) noted that some seasonal bird densities are closely tied to juniper berry production, which suggests that pinyon-juniper woodlands may not provide consistent winter food sources for some species.

Pinyon-juniper ecosystems also provide important habitat for numerous small mammal species. Sureda and Morrison (1999) documented several small mammal species associated with pinyon-juniper woodlands in Utah, including pinyon mice (*Peromyscus truei*), mexican woodrats (*Neotoma mexicana*), and Colorado chipmunks (*Tamias quadrivittatus*). Rompola and Anderson (2004) studied three rare small mammal habitat associations in pinyon juniper woodlands; they found that cliff chipmunks (*Tamias dorsalis*) selected pinyon-juniper habitats in rocky cliffs, pinyon mice favored pinyon-juniper forests with high tree cover and high forb cover, and canyon mice (*Peromyscus crinitus*) preferred cliffs with high forb, rock, and tree cover. Rodhouse et al. (2010) also found that pinyon mice and cliff chipmunks favored habitats with high tree cover near rocky cliffs, but that these species also selected sites with low forb and shrub cover. These studies suggest that small mammal pinyon-juniper habitat selection is partially context dependent; however, a few habitat associations are consistently observed. For instance, the pinyon mouse has shown a strong affiliation to mature woodland habitats, whereas deer mice have demonstrated an affinity for sites that are relatively open, with more shrubs and grasses than trees (Holbrook 1978). Thus, heterogeneous cover of pinyon-juniper woodlands may provide habitat for multiple small mammal species.

Studies of other mammals in pinyon-juniper ecosystems are less common. Chung-MacCoubrey (2005) found that bat diversity was higher in pinyon-juniper woodlands than in

ponderosa pine forests in New Mexico, and that pinyon-juniper woodlands may provide important breeding habitat for bats. Porcupines (*Erethizon dorsatum*) also use pinyon-juniper woodlands, and have been observed foraging under junipers or on juniper bark (Sweitzer 1996). Pinyon-juniper ecosystems may also supply critical wintering habitat for mule deer (*Odocoileus hemionus*) by providing thermal and security cover (Bender et al. 2007, Anderson et al. 2012). Pinyon-juniper woodlands could additionally provide important elk (*Cervus elaphus*) habitat, particularly by providing bedding sites (Bender et al. 2012).

Information on hepatofauna or arthropod pinyon-juniper habitat relationships is limited. Three species of phrynosomatine lizards (*Urosaurus ornatus*, *Uta stansburiana*, and *Sceloporus undulatus*) use pinyon-juniper habitats, particularly rocky outcrops within pinyon-juniper woodlands (James and M'Closkey 2004). Long-nosed leopard lizards (*Gambelia wislizenii*) also prefer juniper and sage dominated habitat, and are thought to prey on insects that feed on juniper (Schorr et al. 2011). Brantley and Shepherd (2004) found 34 species of arthropods on cryptobiotic soil crusts in pinyon-juniper woodlands, including mites, collembolans, diplurans, pseudoscorpions, thrips, tardigrades, nematodes.

Changes in Pinyon Juniper Woodlands

Pinyon-juniper (*Pinus* and *Juniperus* spp.) woodlands currently cover 19 to 20 million ha of land in the United States (Gottfried et al. 1995, Lowry et al. 2007) and are the third most extensive plant community in the country (West 1984). Pinyon-juniper woodlands in the intermountain west have experienced considerable shifts in both spatial distribution and tree density since European settlement (West 1988). Pre-settlement woodlands are thought to have been more “savannah-like” compared to the dense overstory that characterizes much of this ecosystem today (West 1988). Data from old-growth stands, tree age-class structures, fire scars

and historical documents all provide evidence indicating pinyon-juniper stands were historically open woodland (West 1984).

The changes that have occurred in pinyon-juniper ecosystems due to post-settlement land use patterns have been well-documented and are summarized below (Blackburn and Tueller 1970, Tausch et al. 1981, West 1984, West and Van Pelt 1987, West 1988, Gottfried et al. 1995, Miller et al. 1995, Miller and Rose 1995, Gruell 1999, Miller and Rose 1999, Tausch 1999, West 1999). Fire historically acted as the primary mechanism for thinning trees, maintaining open conditions and restricting older trees to steep, rocky or fractured landscapes. Fire spread readily through pinyon-juniper stands because of the abundantly distributed fine fuels, particularly grasses, which were targeted by livestock once grazing was introduced to the region. Under severe grazing conditions, the diversity and cover of native grasses diminished leading to a reduction in fire frequency. These conditions, along with the active suppression of natural fires, facilitated thickening of existing canopy cover and the spread of pinyon-juniper woodlands into nearby degraded grasslands and shrub steppe. However, others contend that evidence is lacking to support the conclusion that fire suppression and grazing are the main drivers of pinyon-juniper expansion into sagebrush and grassland ecosystems (Baker and Shinneman 2004). Alternative hypotheses have posited that changes in pinyon-juniper structure and distribution are driven by changing climatic conditions. Johnson et al. (1990) concluded that the expansion of pinyon-juniper woodlands was linked to increased atmospheric carbon dioxide, and Allen and Breshears (1998) attributed expansion of pinyon-juniper into ponderosa pine forest to drought conditions.

Nevertheless, pinyon-juniper stands have expanded and become increasingly dense throughout their range. As a result, the understory shrubs, herbs and grasses in this ecosystem have generally declined in diversity and cover (Blackburn and Tueller 1970, Tausch et al. 1981,

Pieper 1990, Tausch and West 1995, Gottfried et al. 1995, Miller et al. 2000), and the number of understory seeds in the soil seed bank have been reduced (Koniak and Everett 1982, Poulsen et al. 1999). Additionally, the composition of the understory, once dominated by perennial plants, is now primarily annuals, including the highly invasive and widespread cheatgrass (*Bromus tectorum*) (Vaitkus and Eddleman 1991, Bunting et al. 1999, Poulsen et al. 1999).

Pinyon-Juniper Woodland Reduction

The vegetative changes associated with pinyon-juniper expansion have often reduced habitat quality for both wildlife and livestock by reducing forage availability (Short et al. 1977, Short and McCulloch 1977, Tausch and Tueller 1977, Hoenes et al. 2012). The loss of herbaceous cover in the understory may also make these stands more susceptible to soil erosion, with subsequent negative impacts on water quality (Roundy and Vernon 1999). However, others suggest that there is inconsistent evidence on the impacts of increased pinyon-juniper cover on forage quality and erosion properties (Belsky 1996). Nevertheless, perceived potential impacts have prompted land managers to reduce the density or limit the extent of pinyon-juniper woodlands using mechanical methods (chaining or bulldozing), or by fuelwood cutting, fire, or herbicides (Plummer et al. 1968, Aro 1971, Tausch and Tueller 1977, Stevens 1987, Evans 1988, West 1988, Stevens 1999). Historically, chaining has been the method most widely employed by land managers to reduce pinyon-juniper woodlands (Aro 1971, Evans 1988). Evans (1988) reported that over 100,000 acres had been chained by 1988 on land managed by the Forest Service and the Bureau of Land Management. These efforts have had mixed results in terms of successfully reducing tree cover and preventing re-establishment (Tausch and Tueller 1977, Stevens 1987, Evans 1988, Van Pelt et al. 1990, Stevens and Walker 1996). Tausch and Tueller (1977) reported that trees steadily reinvaded and dominated sites within 15 years of treatment,

leading to declines of understory abundance and requiring re-treatment. Evans (1988) also recommended re-treatment to restore habitat and improve forage production in areas previously treated by chaining. However, others did not observe an increase in tree density or re-invasion after treatment, but in contrast, observed declines in tree density up to 30 years post treatment (Stevens 1987, Van Pelt et al. 1990, Stevens and Walker 1996).

Woodland reduction using chaining and similar methods is not necessarily designed or intended to restore native plant communities. Tree removal is often followed by seeding in cases where understory plants are too sparse to provide an adequate stand. In the past, seed mixes typically included a high proportion of non-native grasses, forbs, and shrubs (Stevens 1999). Non-native species were used because they improved forage for cattle, they were easy to establish, and because of limited native seed availability (Stevens 1999). This practice may be counter-productive because the main threats to sagebrush steppe ecosystems include both pinyon-juniper expansion and invasion by non-native grasses (Shinneman and Baker 2009). More recently, non-native species are increasingly being replaced with native plants in seed mixes used by some agencies (Landis et al. 2005).

Consequences of Woodland Reduction for Wildlife

Bird responses to woodland reduction have been studied more than any other taxonomic group. Pavlacky and Anderson (2001) investigated habitat associations for pinyon-juniper obligate birds and found that most of these species favored areas with greater pinyon pine cover and high canopy height; the authors emphasized the importance of maintaining pinyon pine to provide quality habitat for pinyon-juniper specialists. Balda and Masters (1980) also stress retaining pinyon pines because they detected a positive relationship between foliage-feeding and/or cavity nesting birds and pinyon pine density. However, Francis et al. (2011) found that

86% of nests in live trees that belonged to open cup and cavity nesting birds occurred in juniper trees, and recommended that the selective removal of juniper be avoided when thinning woodlands.

Birds of pinyon-juniper woodlands are often broadly classified into two groups: open-area early seral species and late-successional pinyon-juniper woodland species. Rumble and Gobeille (1994) detected trends that suggested higher abundance, diversity, and species richness in both early and late successional stages, which implies that birds are selecting for these extremes along the successional gradient. The authors maintain that intermediate seral stage woodlands are unfavorable to both guilds in being too dense for ground nesters and lacking the height, canopy volume, and structural diversity of mature stands that are preferred by tree-nesters (Rumble and Gobeille 1994). In contrast, others have found that intermediate stages supported higher species richness and diversity values because the transitional habitat in these stages attracted members from both groups; however, they still detected a division in habitat use by early seral and late successional-species (Reinkensmeyer et al. 2007). Sedgwick (1987) also separated species into these groups and found that hermit thrushes (*Catharus guttatus*), plumbeous vireos (*Vireo plumbeus*), and black-throated gray warblers were associated with forest overstory and late-successional pinyon-juniper stands while green-tailed towhees (*Pipilo chlorurus*), spotted towhees (*Pipilo maculatus*), and rock wrens (*Salpinctes obsoletus*) demonstrated preferences for open, early successional habitat characteristics.

Although bird abundance is higher in pinyon-juniper woodlands than in adjacent grasslands (Sieg 1991, Reinkensmeyer et al. 2007), and species richness, diversity, and evenness are relatively low in sage steppe and shrubland habitats (Johnson and Haight 1980, Reinkensmeyer et al. 2007), certain species depend almost entirely upon sage steppe and

grassland habitat structure (Johnson and Haight 1980, Rotenberry and Wiens 1980, Wiens and Rotenberry 1981), making the conservation of optimal proportions of multiple successional stages along the grassland-shrubland-woodland gradient important for landscape-level diversity. Reinkensmeyer et al. (2007) investigated bird community composition in four successional stages: grassland, shrub-steppe, shrub-steppe-juniper (transitional state between shrub-steppe and old-growth juniper), and old-growth juniper. The authors found the highest densities of vesper sparrows (*Pooecetes gramineus*), green-tailed towhees, and western meadowlarks (*Sturnella neglecta*), all ground nesting birds, in grassland vegetation types and rarely detected these species in any vegetation types that included juniper. In shrub-steppe communities, sage sparrows (*Amphispiza belli*), Brewer's sparrows (*Spizella breweri*), sage thrashers (*Oreoscoptes montanus*), and horned larks (*Eremophila alpestris*) were all found in greater densities than in grassland and shrub-steppe-juniper communities, and were not found in old-growth juniper. The shrub-steppe-juniper stage included species from both shrub-steppe and old-growth juniper successional stages, but was not comprised of any species with higher densities than in the other three stages. The greatest densities of birds occurred in the old-growth juniper stage due to the presence of tree and cavity nesting species; however, shrub and grass nesting species were rarely observed in this stage. Similarly, Rosenstock and Van Riper (2001) found that ground-nesting grassland species declined and tree and cavity nesting species increased with higher tree densities in developing pinyon-juniper woodland.

Bird community responses to pinyon-juniper woodland reduction vary, but generally result in decreased species richness and abundance (O'Meara et al. 1981, Sedgwick and Ryder 1987). These negative responses are typically driven by species in the foliage- and cavity-nesting guilds; however, the less dominant ground- and shrub-nesting species typically benefit

from woodland reduction (O'Meara et al. 1981, Sedgwick and Ryder 1987, Crow and van Riper 2010). O'meara et al. (1981) observed over twice as many bird species and double the density of birds in unchained plots compared to plots chained within the previous 8 and 15 years. Similar to the observations of Reinkensmeyer et al. (2007) of bird use in various successional stages, the Green-tailed towhee, the Vesper sparrow, and the Brewer's sparrow, all species associated with grasslands and shrublands, only occurred on the chained plots and avoided the unchained control plots; whereas cavity and tree nesters composed most of the community using unchained plots (O'Meara et al. 1981). Sedgwick and Ryder (1987) similarly found higher bird abundance, species diversity and species richness on untreated pinyon-juniper plots compared with chained plots. Sedgwick and Ryder (1987) also investigated differences in guild responses and found that several foraging or nesting guilds used chained plots significantly less including foliage-and-timber searchers, aerial foragers, foliage nesters, and cavity nesters; however, ground foragers and ground nesters were less impacted by chaining. Bird community responses to thinning methods used by land managers more recently appear to be relatively similar to chaining responses. In mechanically thinned plots, pinyon-juniper obligate species abundance was significantly lower and shrub nester and habitat generalist abundance was significantly higher after treatment (Crow and van Riper 2010). After the removal of young junipers that had invaded sage-steppe habitat used by sage grouse, abundance estimates of male sage grouse on leks doubled (Commons et al. 1999).

Small mammal pinyon-juniper habitat associations and responses to woodland reduction have also been well documented. Rumble and Gobeille (1994) evaluated small mammal habitat use in different seral stages of juniper woodlands along the Missouri River in South Dakota. They found that intermediate seral stages supported more small mammals and had higher species

richness than early or late stages. Specifically, these intermediate stages had higher abundances of deer mice and prairie voles (*Microtus ochrogaster*), while early seral stages favored meadow voles (*Microtus pennsylvanicus*), a grassland species. Horncastle et al. (2005) evaluated small mammal responses to invasion of red cedar (*Juniperus Virginiana*), and found that grassland species decreased as red cedar increased; yet, only one woodland species increased (*Peromyscus leucopus*) with changes in overstory cover from 0 to 30%. This limited information suggests that grassland small mammal species will be adversely affected by woodland expansion and that few small mammal species will benefit from an increase in late seral stage pinyon-juniper woodlands.

Previous research on small mammal responses to woodland removal from chaining or thinning treatments suggests that small mammal numbers increase substantially after woodland removal, however changes in other community estimates (i.e., species richness and diversity) vary (Turkowski and Reynolds 1970, Baker and Frischknecht 1973, O'Meara et al. 1981, Severson 1986, Sedgwick and Ryder 1987, Albert et al. 1994, Kruse 1994, Willis and Miller 1999). Turkowski and Reynolds (1970) found that the higher abundance of rodents on treatment plots on the Kaibab Plateau in Arizona was due to an increase in resident rodent numbers as well as immigration into the treatment area by other species and individuals. Baker and Frischknecht (1973) identified a considerable increase in the number of deer mice and Great Basin pocket mice (*Perognathus parvus*) for the first two years after chaining and seeding pinyon-juniper plots, and although the numbers declined in the following years, the abundance of these species remained above the pre-treatment levels. Long-term patterns of increased small mammal abundance after woodland reduction have also been observed. Severson (1986) found higher total small mammal numbers on 13 to 18-year-old pinyon-juniper treatment plots than on

untreated plots. O'Meara et al. (1981) also observed higher small mammal abundance on 8- and 15-year old chained pinyon-juniper plots than on unchained plots for most species.

Although most studies indicated greater numbers of small mammals on plots after woodland reduction, many authors noted that a significant proportion of the individuals caught were deer mice (O'Meara et al. 1981, Sedgwick and Ryder 1987, Albert et al. 1994, Kruse 1994, 1999). Deer mice comprised 85% of the total species caught in chained plots in Colorado (Sedgwick and Ryder 1987), and the authors concluded that the only species that benefitted from chaining was the deer mouse. Kruse (1994) also found that fuelwood harvest thinning of pinyon-juniper woodlands was mainly beneficial to deer mice because they increased significantly after treatment. Albert et al. (1994) found a dramatic increase in small mammal abundance on thinned pinyon-juniper plots and indicated that this increase was mainly driven by deer mice.

In contrast to deer mouse responses to woodland reduction, the pinyon mouse (*Peromyscus truei*) was negatively impacted by treatments, as evidenced by decreased numbers of mice in treated plots (Turkowski and Reynolds 1970, O'Meara et al. 1981, Sedgwick and Ryder 1987, Albert et al. 1994, Kruse 1994), with the exception of thinned plots (Severson 1986). However, Albert et al. (1994) did detect a decrease in pinyon mouse density on thinned plots. Also, Turkowski and Reynolds (1970) detected a decrease in brush mice (*Peromyscus boylii*) and pinyon mice in treated plots that they attributed to overstory reduction.

Observed patterns of small mammal species richness in chained and unchained plots have been less consistent than species abundance. O'Meara et al. (1981) found higher diversity on plots that were not chained, whereas Sedgwick and Ryder (1987) found greater small mammal species richness on chained plots. These discrepancies may be due to the differences between the species diversity metric, which incorporates evenness and richness, and the species richness

metric. Unchained plots may have greater evenness in species, resulting in a higher diversity value, whereas chained plots might have higher numbers of species overall. However, Severson (1986) did not find a difference in small mammal species richness between bulldozed and untreated plots. Yet, fuelwood harvest thinning of pinyon-juniper was also associated with higher small mammal species diversity (Kruse 1994). These conflicting results may be due to inherent differences within the sampled small mammal communities and due to regional differences between study locations. Willis and Miller (1999) suggested that these differences occur due to heterogeneity in spatial and temporal conditions of western pinyon-juniper woodlands, and due to a lack of consideration of woodland composition before treatments as well as a lack of attention to succession after treatments.

Treatment methods that involve slash piling (trees piled after removal) can also influence small mammal responses. Deer mice and long-tailed voles (*Microtus longicaudus*) demonstrated an affinity for treatment plots where slash was windrowed (Baker and Frischknecht 1973), and both Albert et al. (1994) and Kruse (1999) concluded that slash piling was particularly beneficial to deer mice. Severson (1986) also found that brush mice and woodrats (*Neotoma* spp) preferred sites with slash intact, but that certain species, such as pinyon mice, were more selective and only increased when both slash and intact overstory was present. In contrast, Kruse (1999) found that both slash piling and overstory removal adversely affected pinyon mice, especially in the year immediately after reduction, and Albert et al. (1994) found that pinyon mice decreased in treatment plots even when slash was present. Overall, the pinyon mouse seems particularly sensitive to overstory reduction in spite of slash piling. In addition, the combination of slash piling and the presence of overstory may adversely affect grassland rodents. Severson (1986)

detected lower numbers of grassland rodents on sites where both overstory and slash were present.

Responses of other taxonomic groups to woodland reduction have been poorly studied. Some limited information exists for game species, however. Bergman et al. (2014) found higher overwinter survival of mule deer fawns on treatment areas where pinyon-juniper overstory was removed and plots were reseeded and maintained with weed control. Short et al. (1977) studied mule deer and elk use of pinyon-juniper woodlands cleared with bulldozers and chainsaws, and found that although large-scale clearings increased forage production, they were not attractive to deer or elk due to the loss of protective cover. However, smaller woodland reduction patches that existed within a matrix of protective cover were used more by deer and elk (Short et al. 1977). Thus, Short et al. (1977) recommend reducing pinyon-juniper woodlands in numerous small patches within a matrix of dense woodlands.

Although I was not able to find any research documenting responses of arthropods to woodland reduction, some information exists on early and late successional arthropod assemblages in pinyon-juniper woodlands. Higgins et al. (2014) compared arthropod assemblages in old-growth pinyon-juniper woodlands and burned habitats and found greater total arthropod abundance and species richness in early successional (burned) habitats. They also found that 83 arthropod species were associated with old-growth pinyon-juniper habitat, 62 species were associated with early successional habitat, and 125 species occurred in both habitats (Higgins et al. 2014), which suggests that the benefits and impacts of woodland reduction on arthropod assemblages may be taxon specific. Ditsworth et al. (1982) also compared arthropod assemblages in mature pinyon-juniper woodlands to those on disturbed power-line clearing sites and found a greater diversity of arthropods on disturbed sites, which they attributed to the

composition of the pioneer plant community. They also found that several taxa increased in abundance on disturbed sites (thysanopterans, cicadellids, aphidids, and lepidopterans), whereas others (mites and scale insects) declined (Ditsworth et al. 1982). This limited evidence suggests that woodland reduction may increase the abundance and diversity of several arthropod species, while impacting others.

Future Research Priorities

Previous literature on the effects of woodland reduction on wildlife has been restricted to the methods of chaining, thinning, and burning. Land managers in the western United States are currently employing alternate mechanical reduction and seeding methods, e.g. hydro-axing and roller-chopping, to enhance habitat quality for cattle and game species (Bergman et al. 2014). Although the effects of chaining on wildlife have received some attention, wildlife responses to roller-chopping and hydro-axing methods remain unknown. Yet, these novel methods may be employed frequently in the future to reduce woodlands in many regions because they are more effective in some situations. For example, hydro-axe woodland removal generates negligible soil disturbance, which makes this method particularly useful in situations where archeological sites should remain undisturbed. Future research is needed to compare the effects of these newer methods on non-game wildlife. This research should test for differences among each method experimentally, by applying different woodland reduction treatments at the same time and in the same management area, so that the effects of each treatment strategy can be distinguished from temporal or environmental variation between habitat types.

This literature review has also highlighted a lack of information on the responses of many animal assemblages to woodland reduction. Future research should focus on how poorly-studied taxa, such as reptiles and arthropods, respond to woodland reduction treatments. Such studies

would broaden our understanding of wildlife responses to woodland reduction, which will help land managers make informed decisions about the potential synergies and tradeoffs of woodland reduction strategies for various taxa. Practitioners should identify *a priori* whether both target and non-target species will benefit from woodland reduction, and should make arrangements to monitor potentially impacted species, such as the woodland-affiliates identified in this review. Woodland reduction should also be conducted in an adaptive-management framework so that effectiveness can be evaluated, and practices adjusted, to achieve and maintain desired ecosystem states (Folke et al. 2004).

SUMMARY

Woodland reduction will be increasingly prevalent in pinyon-juniper and sage-steppe ecosystems as woodlands expand and energy development activities threaten prioritized wildlife species. Creative solutions will be needed to reconcile the benefits and costs to wildlife from this form of habitat manipulation. Research can play an important role in guiding the future of these landscapes by providing rigorous ecological studies to support decision-making. Specifically, research is needed to understand how novel woodland reduction strategies will affect multiple taxonomic groups, especially poorly-studied reptile and invertebrate assemblages. Finding ways to implement woodland reduction strategies that target multiple-species conservation objectives remains an important conservation challenge in one of the largest ecosystems in western North America.

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CHAPTER TWO

IMPROVING UNGULATE HABITAT IN A REGION UNDERGOING RAPID ENERGY DEVELOPMENT: CONSEQUENCES FOR SONGBIRDS AND SMALL MAMMALS

INTRODUCTION

The demand for domestic energy along with recent advances in technology is leading to unprecedented energy development in the western U.S. (McDonald et al. 2009). Over 20 million ha of new land are predicted to be converted to energy development activities by 2030 (McDonald et al. 2009). This large-scale transformation of western rural lands is expected to have substantial environmental impacts (Bartis et al. 2005, McDonald et al. 2009, Copeland et al. 2011, Northrup and Wittemyer 2013), especially in the form of habitat loss and fragmentation (McDonald et al. 2009, Northrup and Wittemyer 2013). Potential negative effects on wildlife include direct mortality, displacement, altered behavior and species composition, loss of migratory routes, decreased species richness, diversity, abundance, survival, and reproduction, and increased stress, predation, and illegal hunting (Northrup and Wittemyer 2013). These impacts may also affect our ability to manage game species through hunting in regions where hunting is frequently used as a wildlife management tool (Dyke et al. 2011).

Mitigation for the impacts of energy development on terrestrial wildlife often takes the form of habitat manipulation for game species (Van Dyke et al. 2012). Because pinyon-juniper (*Pinus edulis*, *Juniperus* spp.) woodlands are expanding into grassland and shrubland ecosystems across much of the western U.S. (Blackburn and Tueller 1970, Miller and Wigand 1994, Miller and Rose 1995, Miller and Rose 1999), impacting herbaceous plant and shrub diversity and

cover (Miller and Wigand 1994, Tausch and West 1995, Miller et al. 2000), habitat mitigation in these systems is largely focused on reducing pinyon-juniper woodland extent and stand density (Plummer et al. 1968, Stevens 1987). These efforts are primarily intended to restore a shrub, herb and grass community that benefits mule deer as a compensatory mitigation strategy to offset impacts from energy development. Yet woodland reduction is also a form of land use change, and the effects of this type of habitat mitigation on other wildlife species are not well understood, especially in the context of energy development. Habitat mitigation intended to benefit a target species may differentially affect non-targeted species, and nearby energy exploitation may exacerbate impacts to some wildlife populations. To sustain diverse native animal assemblages in these ecosystems, it is critical to understand the consequences of species-specific habitat mitigation, and to identify effective strategies for the conservation of multiple species in energy development-impacted landscapes.

Literature on the effects of pinyon-juniper woodland reduction on non-targeted wildlife species has focused on traditional methods such as chaining, thinning, and burning (Turkowski and Reynolds 1970, Baker and Frischknecht 1973, O'Meara et al. 1981, Severson 1986, Sedgwick and Ryder 1987, Albert et al. 1994, Kruse 1994, Willis and Miller 1999, Crow and van Riper 2010). The effects of novel woodland reduction methods, including hydro-axing and roller-chopping, and how wildlife respond to the vegetative and structural changes associated with these habitat mitigation treatments remain unknown. Yet, treatments such as hydro-axe, roller-chop, and chaining result in very distinct post-treatment habitat conditions (Fig. 1). Novel hydro-axe and roller-chop treatments are increasingly being used by land managers to improve ungulate habitat in regions impacted by energy development, with little experimental evidence on the comparative effects of these alternative methods on wildlife. Since these treatments are

predicted to result in different vegetation composition and structure, and unique microclimatic conditions, understanding the effects of these alternative forms of habitat mitigation on non-game species assemblages is both ecologically interesting and has important conservation implications.

In response to energy development impacts on game species, and the need for information on economically and logistically effective methods for mitigating these impacts, a series of experimental treatment plots were established in the Piceance Basin (Fig. 2), a region of Colorado undergoing rapid energy development. The Piceance Basin provides habitat for one of the largest migratory mule deer herds in North America (White & Lubow 2002, Lendrum et al. 2012), and deer hunting is an important component of the local economy. Habitat mitigation in the region is thus largely driven by concerns that intensifying energy development is having negative impacts on this important herd (Anderson 2013). I used the experimental treatment plots in this region to additionally test the initial effects of different habitat mitigation treatments on songbird and small mammal assemblages. Specifically, I measured species occupancy and species richness for both taxa, and density for some small mammal species in each treatment and control plot in the two years following the establishment of the experiment (bird data were only collected in the second year). I also evaluated songbird and small mammal site use as a function of various habitat characteristics to determine what habitat components animals are initially selecting in each treatment. By analyzing both the effect of habitat mitigation treatments and habitat selection within treatments, I can identify habitat mitigation strategies that maximize benefits to multiple species by supporting specific habitat characteristics preferred by songbirds and small mammals.

Incorporating habitat components that benefit birds and small mammals into mitigation strategies for game species is desirable. These species provide ecological services such as seed dispersal and soil aeration, and they can play an important role in structuring plant communities (Vander Wall 1997, Hollander and Vander Wall 2003, Whelan et al. 2008, Garcia et al. 2010, Kelt 2011). There is also real potential for some regional wildlife, especially grassland songbirds, to become species of conservation concern in the face of widespread energy development and land use change in the intermountain west (Gilbert and Chalfoun 2011).

My hypotheses for how habitat mitigation for game species will initially affect songbirds and small mammals are based on the expected differences in post-mitigation vegetation structure and composition among the treatments. Since previous literature indicates that woodland removal generally reduces bird species richness and abundance (O'Meara et al. 1981, Sedgwick and Ryder 1987), I hypothesized that, for the bird community, species occupancy and richness values would be greater in the control plots than in all habitat mitigation treatment plots, and there would be no differences in occupancy and richness among the three treatment methods; bird use of plots will primarily be associated with percent tree cover and not other differences in habitat components between the habitat mitigation treatments. Alternatively, I hypothesized that bird species occupancy and richness values would differ among control plots and all treatment plots. I predicted that bird species occupancy and richness would follow a gradient of the vegetative structural complexity associated with the post-treatment conditions (control > chaining > roller-chop > hydro-ax). I expected that birds would prefer sites with greater vegetation cover and structural complexity (Fig. 1), since habitat components such as percentage of shrub and tree cover provide structure for perching, nesting and foraging sites in pinyon-juniper woodlands (Sieg 1991). To further refine these predictions, I expected the strength of the

response to mitigation treatments to vary by functional groups: dense woodland birds would respond negatively, open woodland birds would respond neutrally, and shrubland/grassland birds would respond positively, as has been found in other studies of the effects of chaining, bulldozing or thinning pinyon-juniper woodlands on birds (O'Meara et al. 1981, Sedgwick and Ryder 1987, Crow and van Riper 2010).

I also hypothesized that small mammals would respond positively to all mitigation treatments (higher species occupancy, density, and richness in all treatment types vs. controls, with no differences between treatment types), given that previous literature indicates a positive relationship between small mammal abundance and slash cover (Baker and Frischknecht 1973, Severson 1986, Albert et al. 1994, and Kruse 1999). Since slash was not removed or burned post-treatment, I expected increased slash or woody debris cover in all treatments compared to control areas to support higher small mammal occupancy, density, and species richness. Alternatively, I hypothesized that small mammal occupancy, density, and species richness values would differ between controls and the three different treatment types. I predicted that species occupancy, density, and richness would follow a gradient of slash cover associated with each mitigation treatment (chaining > roller-chop > hydro-axe > control), since I expected that each treatment would generate distinct levels of slash (Fig. 1) and that small mammals would respond to these differences. On the other hand, small mammal occupancy or density and species richness values may follow a gradient of grass, shrub, and forb cover associated with each mitigation treatment, given that many small mammals in pinyon-juniper woodlands are seed predators (Vander Wall 1997, Hollander and Vander Wall 2004) and their response to treatments may be primarily driven by food availability.

METHODS

Study Area

This study was conducted in the Piceance Basin, northwest Colorado. The Piceance Basin is particularly well-suited to address research questions about how habitat mitigation for energy development impacts animal population and community dynamics. This region is underlain by the Green River Formation, which contains vast reserves of coal, natural gas, and oil shale that have made it the target of intense energy development. Development activities have altered habitats of desirable game species, such as mule deer (Lendrum et al. 2012), resulting in large-scale habitat mitigation actions (Anderson 2013) that have unknown consequences for birds and small mammals. Dominant land use activities include energy resource extraction and grazing (U.S. Bureau of Land Management 1984). Topography in the Piceance Basin ranges from high plateaus to deeply incised valleys. The arid steppe climate of the Piceance Basin shifts dramatically, both spatially and temporally, due to variation in topography and vegetation cover (Wymore 1974). Vegetation cover in the Piceance Basin varies from bottomland irrigated pastures and croplands to upland sagebrush and pinyon-juniper woodland, or higher-elevation spruce, fir, and aspen forest communities (Wymore 1974, Lendrum et al. 2012). Irrigated lowlands represent <1% total cover, whereas upland pinyon-juniper and sagebrush communities characterize the dominant cover type (35% and 32%, respectively) (Wymore 1974). Woodlands are dominated by two tree species, pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) (Sedgwick 1987, Lendrum et al. 2012).

Study Design and Site Selection

The habitat mitigation treatment plots were established in two adjacent sites in the Piceance Basin known as North and South Magnolia. Although mule deer may co-mingle across

these sites during the winter, the deer on each site migrate to distinct home ranges in the summer (Anderson 2013). The plots were selected using topographic maps and aerial imagery and were ground-truthed to ensure that they met the primary project objective of testing the most effective means of improving mule deer habitat (Anderson 2013). Tracts deemed suitable typically contained younger trees in dense stands and robust understory communities, which would provide a strong growth response after treatment. The stands were composed primarily of pinyon pine and Utah juniper (*Juniperus osteosperma*), and the understory was dominated by Utah serviceberry (*Amelanchier utahensis*), bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpos albus*), mountain mahogany (*Cercocarpus montanus*), and big sagebrush (*Artemisia tridentata*). All plots were established on slopes $\leq 30\%$ and primarily north-facing aspects. The plots ranged in elevation from 2000 to 2165 m. Historical climate records (1981-2010 thirty year average) from the Western Regional Climate Center at the nearby Little Hills Station (station #055048) indicate that total annual precipitation in the area averages 43 cm, and average monthly temperatures can range from -18°C lows in January to 29°C highs in July. The final study design included four adjacent polygons in North Magnolia, and three separate polygons in South Magnolia (Fig. 2). Each polygon was then divided into four plots of roughly equal size (1.0 ha), and mechanical treatments (control, chaining, hydro-ax, and roller-chop) were randomly assigned to each plot. This design resulted in 28 plots of seven replicates each, including the control treatment.

Bird Surveys

Birds were surveyed by conducting 5 minute point counts at 28 count stations placed in the center of each plot (seven per treatment). Each of the 28 stations was surveyed twelve times from 0600 to 0900 in June 2013 and all unique detections of birds seen or heard within plots

were included in counts. Survey covariate data (observer, time of survey, wind, gusts, and cloud cover) and site covariate data (treatment type and site) were also collected. Surveys were not conducted during periods of rain, fog, or high winds (>13 km/hr).

Small Mammal Surveys

Small mammals were live-trapped during June-July 2012 and July 2013 on trapping grids in all 28 plots following protocol established by the American Society of Mammalogists (Sikes et al. 2011). I placed 50 baited (rolled oats, bird seed, and peanut butter) Sherman live traps in each plot and trapped animals between 1800 and 1100 h over four consecutive nights. Captured animals were weighed, identified to species, sexed, marked with two uniquely numbered ear tags (National Band and Tag Company, Newport, KY), and released at the capture location. I also used fluorescent tracking methods (Lemen and Freeman 1985) in July-August 2013 to obtain movement data for small mammal species. Animals were trapped before their activity period, coated in uniquely colored non-toxic fluorescent pigment powders (DayGlo Color Corp., Cleveland, OH), and released. The animals deposited a trace of fluorescent pigment on all encountered objects and left a trail that extended over 300 m, which was detected the following night with a UV torch. Individual tracks were recorded using a GPS. Tracking was not conducted while traps were open and bait was available to avoid the possibility of obtaining misleading animal movement patterns. These data were used to estimate the probability of availability from White and Shenk (2001), which was also used to adjust density estimates (described below) to reflect an animal's availability within plots.

Vegetation Surveys

To test the importance of vegetation characteristics for bird and small mammal occupancy and habitat selection, I collected data on understory plants and ground cover at 10

random subplots (July-August 2012) and 16 random subplots (July-August 2013) within each of the 28 plots. I sampled percent cover of bare soil, rock, litter, wood/slash, mulch, tree, shrub, grass, and forb cover in 1-m² sample frames (0.5 m x 2 m) at four different height classes (0-30 cm, 40.1-80 cm, 80.1-137cm, and 137 cm+) using the ocular cover method to the nearest quarter percent (Korb et al. 2003). I collected overstory data in 2012 in three random 10 x 20 m subplots within each of the 28 plots. I tallied all shrub and tree species and used the ocular cover method to estimate percent cover of both live and dead vegetation at six different height classes (0-0.5 m, 0.6-1 m, 1.1-2 m, 2.1-5 m, 5.1-10 m, >10 m).

Data Analysis: Species Richness

To assess differences in diversity among treatments, I calculated species richness in each treatment type for each taxonomic group using an estimator that accounts for unseen species. I determined my sampling coverage with program *SimAssem* (Reese et al. 2013) and used the estimated range of sampling coverage to choose the appropriate species richness estimator via the choice paths outlined by Brose et al. (2003).

Data Analysis: Birds

To test for differences in use of treatment plots by birds, I used the multi-species approach of Alldredge et al. (2007) to construct single season occupancy models (Mackenzie et al. 2002, 2003, 2006) to compare estimates of occupancy, or the probability of a treatment site being occupied by a given species, among treatments, and to estimate detection, or the probability of detecting at least one bird in a population of N birds that use each treatment type. Models included my main predictor variables and other variables that I expected to explain variation in occupancy or detection based on my a priori hypotheses (Appendix 1). Any

variables that were correlated or were explained by the variation in treatments were not included in my model set.

I used program R (RDevelopmentCore Team 2007) with package RMark (Laake and Rexstad 2008) to construct models based on predictor variables for program MARK (White and Burnham 1999). Model selection and ranking was based on QAICc values, with small sample size and overdispersion correction (Burnham and Anderson 2002, MacKenzie and Bailey 2004). I calculated the difference in QAICc values between the most parsimonious model and other models in the model set (ΔQAICc) and calculated model QAICc weights (w) (Burnham and Anderson 2002, Anderson 2008). For each main effect, I calculated cumulative model weights as the sum of w 's from all models that included the effect (Burnham and Anderson 2002, Anderson 2008). I also calculated model-averaged occupancy estimates and 95% confidence intervals (Burnham and Anderson 2002, Anderson 2008) for each species to assess differences in bird occupancy among treatments. I included both main-effects only models and models that incorporated interactions between the other predictor variables and the "Species" covariate (occupancy varies by species) or the "Habitat guild" covariate (occupancy varies by habitat guilds) (Appendix 1). I ran all possible model combinations of predictor variables, and models with variables that did not converge were dropped from the model set (Appendix 1, Supplemental 1). Guild-based estimates were produced using the highest-ranking model that included a habitat guild effect on occupancy. To assess relationships between habitat guilds and treatments, I used the regression coefficient values from the highest-ranking model to calculate the difference between regression coefficients for the control and treatments, or the effect size (how much occupancy differs in treatments compared to controls). Estimates of standard errors for effect sizes were calculated using the delta method.

Since bird home ranges likely extend beyond treatment plot boundaries, I was unable to meet the occupancy model assumption that a sampling unit (treatment plot) is closed to immigration or emigration, so I redefine my interpretation of bird occupancy to refer to habitat use of treatment plots by birds. Occupancy models also assume that sampling units are independent. To address potential lack of independence among plots that arose from a lack of control over the study design, I have taken the following measures: 1) all observers were careful to only include birds that were observed using the plots during surveys (flyovers or birds that flew in from other areas were excluded), and 2) I used a parametric bootstrap procedure to estimate overdispersion from my most general model (MacKenzie and Bailey 2004) and adjusted my model selection results and model-averaged parameter estimates by this estimate. I also modeled overdispersion because I have reason to believe that birds were not acting independently during surveys (i.e. flocks and mated pairs were present).

Data Analysis: Small Mammals

I analyzed small mammal data using two different approaches. For most small mammal species, I did not have sufficient captures to estimate density, so I used the multi-species approach of Alldredge et al. (2007) to construct multiple-season occupancy models (Mackenzie et al. 2002, 2003, 2006) to estimate species detection probabilities and occupancy among treatments. These models also included an epsilon parameter for the probability that a treatment site becomes unoccupied between years, but since my interest was mainly in how treatments and other factors affected occupancy I only included species or constant covariate effects on epsilon so that I could focus on estimating other parameters. Small mammal occupancy analyses were conducted as described above for bird occupancy analyses, with the following exceptions: 1) since a goodness of fit test is currently not available for multiple-season occupancy models, I did

not calculate an over-dispersion estimate; 2) I did not expect a large enough diversity of small mammal species to create meaningful habitat guilds, and thus did not consider a guild-level response to treatments; and 3) I incorporated different predictor variables in my models based on different a priori hypotheses for small mammals, that resulted in a distinct model set (Appendix 1, Supplemental 1).

Because deer mice (*Peromyscus maniculatus*) are so prevalent, I needed a finer-scale response variable than occupancy for this species. I used Huggins closed capture models and a variance components analysis (White and Burnham 1999) to obtain derived mean estimates of deer mouse abundance for each treatment in both 2012 and 2013. I also used these models to estimate the probability that an animal will be initially captured and the probability of recapture, conditional on an animal having been captured at least once before. I then used the estimated abundance with the area of the plots and the estimate of the probability of availability described earlier to produce an estimate of density (corrected for the proportion of time an animal spends in treatment plots) following the approach of White and Shenk (2001). Lastly, I tested for relationships between treatments or other predictor variables and deer mouse density using a variance components analysis of derived abundance parameters in program MARK (White and Burnham 1999). I used a variance components analysis to explain the biological process variation alone, excluding the sampling variation or the sampling covariation between the plot abundance estimates (Burnham and White 2002). During the variance components procedure, some plots were excluded due to lack of convergence (two hydro-axe, two controls, and one chain plot from 2012; two controls and one chain plot from 2013).

Data Analysis: Habitat Selection

I conducted a separate analysis to assess habitat selection by birds and small mammals by running a second occupancy analysis for both taxonomic groups that focused on estimating occupancy as a function of vegetation and substrate cover covariates (Appendix 2). Since these covariates were associated with the habitat mitigation treatments, I could not include them in my habitat mitigation treatment comparison analysis. Thus, I separately evaluated treatment plot use based on the vegetative and substrate characteristics of plots, irrespective of what treatment was applied. For both taxonomic groups, I constructed multi-species (Alldredge et al. 2007) occupancy models (Mackenzie et al. 2002, 2003, 2006) to estimate occupancy and detection probabilities and used AIC model selection (Burnham and Anderson 2002) to rank models with different vegetation and substrate predictor variables (Appendix 2). All analyses were conducted using program R (RDevelopmentCore Team 2007), package RMark (Laake and Rexstad 2008), and program MARK (White and Burnham 1999). Models included main-effects and interactions between the vegetation or substrate predictor variables and the “Species” or “Habitat guild” covariates (Appendix 2). I ran all possible model combinations of predictor variables, and models with variables that did not converge were dropped from the model set (Appendix 2, Supplemental 1). For all continuous vegetation and substrate effects, I interpreted regression coefficient relationships with occupancy from the highest-ranking model that included the effect. I also computed predicted occupancy values for a range of vegetation and substrate cover values using the estimates from the highest-ranking model that included each vegetation or substrate effect and produced plots of predicted occupancy as a function of each of these habitat components. I separately tested for relationships between habitat variables and deer mouse

abundance using a variance components analysis in program MARK (White and Burnham 1999).

RESULTS

I detected a total of 39 bird and five small mammal species in the habitat mitigation treatment and control plots (Appendix 3, Appendix 4). Of these, 17 bird species and one small mammal species were detected too infrequently to provide sufficient data for occupancy models, and were only used to estimate species richness.

Species Richness

Based on the selection framework of Brose et al. (2003), which uses the percent of sampling coverage for bird surveys in each treatment (Control: 64.51%; Chaining: 43.79%; Hydro-axe: 40.78%; Roller-chop: 49.24%), the second-order jackknife estimator (Burnham and Overton 1979) was the most appropriate species richness estimator for comparisons across all treatments. Estimated bird species richness values varied between treatments and controls, but 95% confidence intervals overlapped (Control: 44.00 (95% CI 36.93-68.12); Chaining: 39.00 (95% CI 28.81-60.98); Hydro-axe: 34.00 (95% CI 24.55-55.26); Roller-chop: 16.00 (95% CI 12.61-38.11)). For small mammals, sampling coverage was large (Control: 91.32%; Chaining: 81.60%; Hydro-axe: 85.55%; Roller-chop: 88.78%), suggesting the use of the first-order jackknife estimator (Burnham and Overton 1979, Brose et al. 2003). Small mammal species richness values were greater in chaining and control plots than in hydro-axe and roller-chop plots, but 95% confidence intervals overlapped (Control: 5.08 (95% CI 5.00-6.87); Chaining: 5.21 (95% CI 5.01-7.95); Hydro-axe: 4.14 (95% CI 4.00-6.27); Roller-chop: 4.08 (95% CI 4.00-5.87)).

Bird Occupancy and Habitat Selection

The parametric bootstrap procedure indicated overdispersion in the data from the bird habitat mitigation treatment models ($\hat{c} = 2.28$), thus I used QAICc values. QAICc model selection results indicated model selection uncertainty for the bird habitat mitigation treatment occupancy models (Appendix 5). Cumulative model weights from the habitat mitigation treatment models indicated that bird occupancy mainly varied by control and habitat guild effects, whereas models with treatment and species effects on occupancy had much less support (Table 1). Models that assumed occupancy was constant across bird species and guilds but varied by main effects of other predictor variables had virtually no support (Table 1).

Model-averaged estimates of species-specific bird occupancy probabilities were notably greater in control plots than in all habitat mitigation treatment plots for most species, but occupancy was only different (CI did not overlap) between control plots and treatment plots for some bird species, particularly birds categorized into dense woodland guilds (Table 2). However, bird occupancy did not differ between the different habitat treatment types (chaining, hydro-axe, or roller-chop) for any species (Table 2). Guild-based estimates from the most parsimonious model in the bird habitat mitigation model set (Appendix 5) indicated similar trends (Fig. 3), but with greater precision to detect differences, gained from sharing information on the detection process (Allredge et al. 2007). Dense woodland birds and open woodland birds had significantly higher occupancy probabilities in control plots than in all treatment plots, but shrubland and grassland bird species occupancy did not differ significantly between treatments and controls. Bird species occupancy did not differ between the three treatment types (chaining, hydro-axe, and roller-chop) for all bird guilds (Fig. 3). Also, dense woodland birds had significantly lower occupancy probabilities in treatment plots than all other guilds (Fig. 3).

These trends were also reflected in the differences between regression coefficients for the controls and treatments (effect size) from the highest-ranking model. The effect of treatments on dense woodland bird occupancy was negative ($\beta_{\text{treatment}} - \beta_{\text{control}} = -3.34$ 95% CI -4.32,-2.35). The effects of treatments on open woodland and shrubland/grassland birds were also negative, but confidence intervals surrounding the effect size estimates overlapped zero (open woodland $\beta_{\text{treatment}} - \beta_{\text{control}} = -1.24$ 95% CI -3.31,0.83; shrubland/grassland $\beta_{\text{treatment}} - \beta_{\text{control}} = -1.24$ 95% CI -3.47,1.00).

Bird species occupancy was associated most strongly with percentage of tree cover over all of the other habitat and substrate characteristics considered in the habitat selection analysis (Table 1). I also found strong support for the habitat guild effect, suggesting that bird habitat associations varied by habitat guilds (Table 1). Regression coefficient (β) relationships between habitat characteristics and bird occupancy also reflect these trends. The directionality of the β estimate for % tree cover suggests higher % tree cover is associated with higher bird occupancy (Table 4), which is also demonstrated in the plot of predicted occupancy as a function of % tree cover (Fig. 5). Additionally, the β estimate and predicted values for % grass and forb cover suggested higher % grass and forb cover was associated with lower bird occupancy (Table 4, Fig. 5). The β estimates for the relationship between bird occupancy and % cover of slash, mulch and bare soil were all negative, but 95% confidence intervals surrounding these estimates overlapped zero (Table 4).

Small Mammal Occupancy and Habitat Selection

AICc occupancy model selection results from the small mammal habitat mitigation treatment models indicated model selection uncertainty (Appendix 5). Cumulative model weights from habitat mitigation treatment models indicated that small mammal occupancy

mainly varied by species and year effects, and only minimally by control or treatment effects (Table 1). Model-averaged estimates of small mammal occupancy probabilities for both 2012 and 2013 did not significantly differ between controls and treatments (Table 2). Based on the treatment effect size estimate ($\beta_{\text{treatment}} - \beta_{\text{control}} = 0.69$ (95% CI -0.43, 1.81)) from the most parsimonious model in the habitat mitigation model set that included a control or treatment effect (Appendix 5), I did not find evidence to indicate that small mammal occupancy is affected by treatments.

Estimates of the probability of availability (\bar{p}) were calculated for small mammals with sufficient tracking data. Least chipmunk (*Tamias minimus*) tracks were mainly confined to the area trapped and thus, least chipmunks had high availability ($\bar{p} = 0.98$ 95% CI 0.95-1.00). Deer mice (*Peromyscus maniculatus*) also had high plot fidelity and availability ($\bar{p} = 0.99$ 95% CI 0.98-1.00).

Deer mouse density estimates (adjusted by probability of availability estimates) were similar across treatments and controls in 2012 and higher in all treatments than in control plots in 2013, but did not differ significantly among treatments or controls for either year based on overlapping confidence intervals (Fig 4). Variance components analysis results from 2012 also did not indicate that treatments had any effect on deer mouse density since almost all treatment or control effects explained no process variance (Table 3). However, in 2013 the control effect explained nineteen percent of the process variance in density estimates (Table 3).

Results from the analysis of small mammal habitat selection suggested that small mammal occupancy was associated with several habitat and substrate characteristics considered in my analysis. Small mammal occupancy in the habitat selection models mainly varied by species, site, and % grass and forb cover; however other habitat effects had some support (Table

1). The directionality of the β estimate and predicted occupancy values for % grass and forb cover indicated a positive relationship between grass and forb cover and small mammal occupancy (Table 4, Fig. 5). The β estimates for the relationship between small mammal occupancy and % cover of slash, mulch and bare soil were also positive, but 95% confidence intervals surrounding these estimates overlapped zero (Table 4). Although the results varied by species, the predicted values showed similar trends between habitat characteristics and different small mammal species occupancy (Fig. 5). Variance components analysis results from the 2013 deer mouse data were similar to the habitat selection occupancy results for other small mammal species in that several habitat characteristics (grass and forb cover, tree cover, slash cover, and mulch cover) explained some of the variability in deer mouse densities (Table 3). However, in 2012, the habitat characteristics explained none of the variance in density estimates (Table 3).

DISCUSSION

Over the two years of my study, habitat mitigation, designed to offset the impacts of energy development on game species, had mixed effects on bird and small mammal species richness, occupancy, and density. I found no significant difference in small mammal species richness, occupancy, or density estimates among treatments (Table 2, Fig. 4). However, treatment plots demonstrated lower bird occupancy compared with control plots for dense woodland and open woodland bird species (Table 2, Fig. 3). I did not find a difference in grassland and shrubland bird occupancy between treatments or controls. These results have important implications for birds and mammals in the large portion of the western U.S. dominated by pinyon-juniper woodland and undergoing energy development and other land use changes.

My findings support previous research on the effects of chaining on wildlife, and provide new information on how wildlife respond to novel and increasingly widely used woodland

clearing techniques (hydro-axe and roller-chop). I found evidence that all habitat mitigation treatment methods (chaining, hydro-axe, and roller-chop) impacted dense woodland and open woodland bird species by reducing site occupancy relative to control areas. Other investigators have found that chaining treatments impacted birds relative to control areas (O'Meara et al. 1981, Sedgwick and Ryder 1987). O'Meara and others (1981) found lower bird densities and Sedgwick and Ryder (1987) found lower bird abundance on chained plots compared with untreated pinyon-juniper plots. My research is the first to demonstrate that novel habitat mitigation treatment strategies (roller-chopping and hydro-axing) have similar impacts to birds as traditional chaining treatments. These results are consistent with my hypothesis that bird occupancy of treatment sites would be primarily associated with tree cover and not other differences in habitat components between treatments. Additional evidence that bird occupancy is primarily associated with tree cover is provided by my habitat selection analysis. The β estimates and predicted values from these models show a positive relationship between % tree cover and bird occupancy across all guilds (Table 4, Fig. 5).

My results supported my hypothesis that bird responses to habitat mitigation treatments would vary by habitat-based guilds. Dense woodland birds and open woodland birds used all habitat mitigation treatment types significantly less than control areas (Fig. 3), but I did not find evidence that shrubland and grassland bird occupancy differed between treatments and controls (Fig. 3). Similar to my findings, Sedgwick and Ryder (1987) found that several woodland-associated bird guilds used chained plots significantly less; however, ground foragers and ground nesters were less impacted by chaining. O'Meara and others (1981) also found that the response to chaining treatments varied by bird guilds. Similar to my results, they found that cavity and tree nesters primarily used the control plots and avoided the chaining plots; however, unlike my

findings, bird species associated with grasslands and shrublands only occurred on the chained plots and avoided control plots (O'Meara et al. 1981). These discrepancies may relate to inherent differences in post-treatment recovery time between my study and that of O'meara et al. (1981). O'meara studied bird responses to chaining in eight- and fifteen-year old chained plots, whereas I evaluated bird responses to chaining, hydro-axing, and roller-chopping in the first two years post-treatment. Positive responses to woodland removal by shrubland and grassland birds may not occur until close to a decade after treatments are established, and thus would not have been detected during the timeframe of my study.

Several studies have found higher small mammal numbers in chained plots than in unchained control plots, but differences were mainly driven by deer mouse abundance (Turkowski and Reynolds 1970, Baker and Frischknecht 1973, O'Meara et al. 1981, Severson 1986, Sedgwick and Ryder 1987). In contrast, results from my occupancy analysis did not indicate a significant difference in small mammal species occupancy or density between habitat mitigation treatments or controls. Although these results were not similar to previous research, I did find non-significant trends of higher species occupancy and density for all small mammal species in all habitat treatments compared to controls (Table 2, Figure 4). Furthermore, my raw data, which are more comparable to results from previous investigators, indicated higher total small mammal numbers in chaining, hydro-axe, and roller-chop treatments compared to control treatments, and these differences often reflected deer mouse abundance (Appendix 6). I also hypothesized that small mammal species occupancy would relate to increases in slash cover associated with tree removal; yet, small mammal occupancy was primarily associated with increases in grass and forb cover. This result supports my alternative prediction that small mammal species occupancy of treatment sites would be associated with food availability. Thus,

higher grass and forb cover may enhance use of habitat mitigation treatment areas by some small mammal species.

Deer mouse density estimates did not follow my prediction that treatments would have a positive effect. In 2012 and 2013, there was no significant difference in densities between treatments and controls; however there was a difference in densities between years (Fig. 4). The temporal differences may have been due to variation in precipitation between years. The Colorado River Basin experienced extreme drought conditions during the August 2012 monsoon season (Palmer Z-Index = -3.45; National Climatic Data Center data from station #502, Colorado River Drainage Basin; values below -1.25 indicate short-term drought and values above 1.00 indicate short term wet periods), and the treatment plots had minimal vegetative growth that year. In contrast, 2013 had normal precipitation during the August monsoon (Palmer Z-Index = 0.02; NCDC data from station #502). As a result, the understory vegetative cover in the habitat mitigation treatment plots increased substantially during the second year of my study. Since the variance components analysis results indicated that grass and forb cover explained some process variance in 2013, increased vegetative cover in the treatments may be associated with higher deer mouse densities in this year.

It is important to note that I conducted small mammal trapping surveys using baited traps. Bait may draw more animals into trapping grids than would occur naturally. Thus, my estimates of density, occupancy, and the probability of availability may be biased. In particular, the probability of availability estimates may not reflect true availability, given that small mammals may be satiated by bait and may not resume their normal foraging activities after being released. Thus, these estimates should be interpreted with caution. However, I do not expect the attraction

to bait or satiation to vary among habitat mitigation treatments, and thus any unintended effects of baiting should not have influenced my treatment comparisons.

Results from my comparisons of bird and small mammal species richness between control and habitat mitigation treatments were partially consistent with previous research on chaining treatments. O'Meara et al. (1981) and Sedgwick and Ryder (1987) found lower bird species richness on chained plots compared with untreated control plots. O'Meara et al. (1981) also reported lower small mammal species richness on chained plots than control plots. My data reflected trends of lower bird and small mammal species richness in all treatment plots (chaining, hydro-axe, and roller-chop) compared to control plots, but I found no significant differences between control or treatment plots. Interestingly, my data also indicated trends of lower bird and small mammal species richness in hydro-axe and roller-chop treatment plots compared with chaining treatment plots; although there were no significant differences in species richness among treatment methods.

This research focused on the initial response of birds and small mammals to habitat mitigation treatments. Future research that assesses long-term wildlife responses to treatments after the vegetation has had time to recover from the initial disturbances would be valuable. Particularly, the currently observed variation in responses to treatments by different bird guilds may become more evident over the long-term. Since shrubland and grassland bird occupancy did not differ significantly between habitat mitigation treatment plots and control plots, these species may recolonize treatment sites more quickly once the early successional plant community fills in, resulting in higher treatment site occupancy than is currently observed. Several authors have found that birds associated with open habitat, such as ground nesting and ground foraging birds, have higher abundance, diversity, and species richness in early and

intermediate successional pinyon-juniper habitats (Rumble and Gobeille 1994, Rosenstock and Van Riper 2001, Reinkensmeyer et al. 2007). Furthermore, if different habitat mitigation treatment strategies result in unique patterns of vegetation regrowth, then long-term wildlife community responses to each treatment strategy may diverge.

I recommend that these experimental sites remain protected from other management actions, such as future thinning, burning, or tree removal, so that long-term wildlife responses to different habitat mitigation strategies can be assessed. I also suggest that investigators conduct research in other regions using a similar experimental approach to determine if my results can be generalized across pinyon-juniper and sage-steppe ecosystems.

Conclusions

Habitat mitigation strategies intended to benefit mule deer have important consequences for birds and small mammals. As observed in this study and by other investigators (O'Meara et al. 1981, Sedgwick and Ryder 1987), many bird species, especially dense woodland birds, are sensitive to several types of habitat mitigation treatments. These species may need to be monitored, especially as energy development continues to impact game species (McDonald et al. 2009, Northrup and Wittemyer 2013), and pinyon-juniper removal is increasingly adopted as a habitat mitigation strategy. Also, since models that included a tree cover effect had strong support in the bird habitat selection analysis (Table 1, Appendix 5), and tree cover is positively associated with occupancy for many pinyon-juniper woodland birds (Table 4, Fig. 5), tree removal strategies that leave some interspersed trees standing to provide structure for birds may be more beneficial than those that clear large contiguous patches of woodland. Lastly, since small mammals responded positively to increased grass and forb cover, mitigation strategies that focus on promoting this cover may benefit some small mammals. Rodhouse et al. (2010) also

found that pinyon-juniper woodlands with greater grass and forb cover supported higher occupancy of certain small mammal species; however pinyon-juniper woodland specialists preferred sites with less forb cover. Thus, increased grass and forb cover may only be beneficial to small mammals in certain contexts. I also found a negative association between grass and forb cover and bird occupancy (Table 4, Fig. 5), but models with grass and forb cover effects had limited support in the bird habitat selection analysis (Table 1, Appendix 5).

The effects of habitat mitigation treatments on multiple species should be considered in a landscape context. My findings and others indicate that pinyon-juniper woodlands are important for many bird species (Sieg 1991, Reinkensmeyer et al. 2007), and that woodland reduction impacts dense woodland and open woodland bird habitat. However, certain bird species depend almost entirely upon sage steppe and grassland habitat (Johnson and Haight 1980, Rotenberry and Wiens 1980, Wiens and Rotenberry 1981), and these species had a neutral response to woodland reduction treatments in my study, and responded positively to treatments in other contexts (O'Meara et al. 1981, Sedgwick and Ryder 1987, Crow and van Riper 2010). Thus, conserving optimal proportions of multiple successional stages along the grassland-shrubland-woodland gradient may promote greater bird diversity in larger spatial contexts. Future research is needed to determine whether landscape-scale woodland reduction strategies that promote landscape heterogeneity, such as treatment methods that leave some standing trees, or treatments that occur as small patches in a mosaic of pinyon-juniper woodlands, increase the conservation value of habitat mitigation treatment areas for non-targeted wildlife. Carefully planned and monitored habitat mitigation will be needed to promote the conservation of multiple species in energy-development impacted landscapes.

TABLES

Table 1. Main effects of predictor variables with cumulative model weights > 0.01 for bird and small mammal habitat mitigation treatment occupancy models (Treat columns) and bird and small mammal habitat selection occupancy models (Habitat selection columns). Main effects related to bird or small mammal occupancy (ψ) and detection of birds or small mammals (p): parameter varies by all habitat treatments (Treatment), by controls vs. treatments (Control), by habitat-based guilds for bird models only (Habitat guild), by species (Species), by detection-based guilds (Detection guild), by year of sampling for small mammal models only (Year), by survey occasion for small mammals only (Survey occasion), by study site (Site), by % cover of grasses and fobs (Grassforb cover), by % cover of trees (Tree cover), by % cover of slash (Slash cover), by % cover of mulch (Mulch cover), or by % cover of bare soil (Bare soil cover). Effects with cumulative weights < 0.01 are either not shown (Observer, Wind, Cloud, Survey time, and Constant effects) or are reported with a dash when shown. NA indicates that the main effect was not included in the specified model set for the specified parameter.

Main effect	Bird cumulative model weights				Small mammal cumulative model weights			
	Treat ψ	Treat p	Habitat selection ψ	Habitat selection p	Treat ψ	Treat p	Habitat selection ψ	Habitat selection p
Treatment	0.09	0.16	NA	NA	0.05	-	NA	NA
Control	0.91	0.83	NA	NA	0.19	-	NA	NA
Habitat guild	0.78	NA	0.72	NA	NA	NA	NA	NA
Species	0.12	-	0.26	0.74	0.99	0.99	0.96	0.99
Detection guild	NA	0.99	NA	0.26	NA	-	NA	-
Year	NA	NA	NA	NA	0.49	0.98	-	0.97
Survey occasion	NA	NA	NA	NA	-	0.02	-	0.03
Site	-	-	-	-	-	-	0.30	-
Grassforb cover	NA	NA	-	NA	NA	NA	0.28	-
Tree cover	NA	NA	0.99	0.99	NA	NA	0.05	-
Slash cover	NA	NA	-	NA	NA	NA	0.07	-
Mulch cover	NA	NA	-	NA	NA	NA	0.05	-
Bare soil cover	NA	NA	-	NA	NA	NA	0.08	-

Table 2. Model-averaged estimates of occupancy probabilities (ψ) for common birds and small mammals found in experimental mule deer habitat mitigation treatment and control plots (n = 7 plots/treatment or control, 28 total) in the Piceance Basin, northwest Colorado. Bird data were collected in June 2013 and small mammal data were collected during June-July 2012 and July 2013. Only 2013 small mammal results are shown (occupancy values were similar between 2012 and 2013). Letters indicate habitat guilds assigned to each bird species (DW = dense woodland birds, OW = open woodland birds, GS = grassland/shrubland birds). Small mammal diversity was too low to construct habitat guilds. *Indicates significant difference between controls and treatments based on non-overlapping maximum likelihood-based 95% confidence intervals.

Species	ψ (95% CI)			
	Control	Chaining	Hydro-axe	Roller-chop
<u>Birds</u>				
Mourning dove ^{GS}	0.73 (0.34-0.94)	0.41 (0.12-0.78)	0.41 (0.12-0.78)	0.40 (0.12-0.77)
Black-chinned hummingbird ^{OW}	0.72 (0.39-0.91)	0.41 (0.06-0.88)	0.41 (0.06-0.89)	0.41(0.05-0.90)
Broad-tailed hummingbird ^{OW}	0.69 (0.41-0.88)	0.31 (0.16-0.53)	0.31 (0.15-0.52)	0.30 (0.15-0.52)
Hairy woodpecker ^{OW}	0.71 (0.40-0.90)	0.34 (0.12-0.66)	0.34 (0.12-0.65)	0.33 (0.12-0.65)
Northern flicker ^{OW}	0.71 (0.40-0.90)	0.33 (0.14-0.61)	0.32 (0.13-0.60)	0.32 (0.13-0.59)
Ash-throated flycatcher ^{OW}	0.67 (0.37-0.87)	0.30 (0.13-0.55)	0.30 (0.13-0.55)	0.29 (0.13-0.55)
Empid flycatchers ^{OW}	0.70 (0.42-0.88)	0.32 (0.16-0.52)	0.31 (0.16-0.52)	0.31 (0.15-0.52)
Plumbeous vireo ^{DW}	0.68 (0.36-0.89)*	0.12 (0.03-0.37)	0.12 (0.03-0.35)*	0.12(0.03-0.34)*
Western scrub-jay ^{GS}	0.72 (0.33-0.93)	0.34 (0.12-0.66)	0.33 (0.12-0.65)	0.33 (0.12-0.65)
Violet-green swallow ^{OW}	0.72 (0.40-0.91)	0.38 (0.15-0.67)	0.37 (0.15-0.66)	0.36 (0.15-0.65)
Mountain chickadee ^{DW}	0.70 (0.40-0.89)*	0.14 (0.04-0.40)*	0.13 (0.04-0.38)*	0.13 (0.04-0.37)*
Juniper titmouse ^{OW}	0.65 (0.27-0.90)	0.30 (0.12-0.56)	0.30 (0.12-0.56)	0.29 (0.12-0.56)
White-breasted nuthatch ^{OW}	0.68 (0.42-0.87)	0.31 (0.15-0.53)	0.30 (0.15-0.53)	0.30 (0.14-0.53)
Blue-gray gnatcatcher ^{DW}	0.67 (0.32-0.89)	0.12 (0.03-0.37)	0.12 (0.03-0.35)	0.12 (0.03-0.35)
Mountain bluebird ^{GS}	0.72 (0.36-0.92)	0.35 (0.16-0.60)	0.34 (0.15-0.60)	0.33 (0.15-0.59)
Black-throated gray warbler ^{DW}	0.72 (0.39-0.91)	0.17 (0.03-0.57)	0.16 (0.03-0.55)	0.16 (0.03-0.53)
Spotted towhee ^{GS}	0.68 (0.32-0.91)	0.32 (0.12-0.62)	0.31 (0.12-0.61)	0.31 (0.11-0.61)
Chipping sparrow ^{OW}	0.72 (0.40-0.90)	0.36 (0.17-0.61)	0.36 (0.17-0.60)	0.35 (0.17-0.59)
Dark-eyed junco ^{DW}	0.71 (0.38-0.91)	0.15 (0.02-0.61)	0.15 (0.02-0.59)	0.14 (0.02-0.57)
Cassin's finch ^{OW}	0.71 (0.41-0.90)	0.35 (0.19-0.55)	0.34 (0.19-0.54)	0.33 (0.18-0.54)
Red crossbill ^{DW}	0.64 (0.24-0.91)	0.12 (0.03-0.38)	0.11 (0.03-0.37)	0.11 (0.03-0.36)
Evening grosbeak ^{DW}	0.68 (0.36-0.89)*	0.12 (0.03-0.37)	0.12 (0.03-0.35)*	0.12 (0.03-0.34)*
<u>Small mammals</u>				
Least chipmunk	0.97 (0.68-0.99)	0.98 (0.78-0.99)	0.97 (0.78-0.99)	0.97 (0.76-0.99)
Uinta chipmunk	0.66 (0.39-0.85)	0.70 (0.50-0.85)	0.70 (0.50-0.84)	0.69 (0.49-0.84)
Golden-mantled ground squirrel	0.76 (0.43-0.93)	0.80 (0.57-0.92)	0.80 (0.56-0.92)	0.79 (0.55-0.92)

Table 3. Variance components analysis of different predictor variables of mule deer habitat mitigation treatment plots and associated estimates of deer mouse abundance from data collected in 2012 and 2013 in the Piceance Basin, Colorado. The mean model process variance was 3.93 (95% CI 1.71-11.64) in 2012 and 363.90 (95% CI 180.58-863.03) in 2013. Each predictor variable was run singly. Negative values for the percent of variance explained are due to different degrees of freedom used in calculating variances of each predictor variable and are regarded as zero.

Predictor variable	Variance 2012 (95% CI)	% of	Variance 2013 (95% CI)	% of
		Variance Explained 2012		Variance Explained 2013
Control	6.61 (2.67-18.16)	-0.68	293.47 (126.05-782.55)	0.19
Chaining	7.49 (2.96-20.38)	-0.90	385.62 (189.04-925.12)	-0.06
Hydro-axe	6.26 (2.45-18.21)	-0.59	360.01(175.77-864.43)	0.01
Roller-chop	7.42 (3.00-20.34)	-0.89	376.35(184.50-913.37)	-0.03
Site	6.62 (2.48-19.12)	-0.68	384.68 (189.34-926.74)	-0.06
Grass & forb cover	7.63 (3.03-0.39)	-0.94	287.21 (171.49-554.93)	0.21
Tree cover	7.02 (2.87-18.29)	-0.78	305.87 (183.06-590.00)	0.16
Slash cover	7.71 (3.17-19.95)	-0.96	287.21(171.49-554.93)	0.21
Mulch cover	7.70 (3.11-20.48)	-0.96	298.14 (178.47-575.00)	0.18
Bare soil cover	7.79 (3.16-20.62)	-0.98	342.43 (205.79-658.52)	0.06

Table 4. Regression coefficient (β) relationships between habitat characteristics and bird or small mammal occupancy probabilities from separate multi-species occupancy analyses of each taxonomic group. β estimates are derived from the highest-ranking model in the model set containing the effect.

Habitat predictor variable	Birds	Small mammals
	β (95% CI)	β (95% CI)
Grass & forb cover	-14.40 (-25.32,-3.47)	9.76 (9.59,9.93)
Tree cover	2.77 (1.65,3.90)	-0.04 (-2.43,2.34)
Slash cover	-1.98 (-4.32,0.36)	1.34 (-2.03,4.71)
Mulch cover	-0.55 (-1.82,0.73)	0.28 (-3.66,4.22)
Bare soil cover	-0.94 (-3.46,1.58)	1.97 (-2.50,6.44)

FIGURES



Fig. 1. Pinyon-juniper removal using different mitigation treatment methods (left photos) and examples of post-treatment conditions (right photos) in experimental plots cleared with a) chaining, c) roller-chopping, and e) hydro-axing. Chaining involves dragging an anchor chain connected to two tractors across a stand, toppling trees (a), and produces plots with abundant slash and small standing trees and shrubs (b). Roller-chopping involves dragging a heavy drum with attached blades behind a tractor; the weight of the drum crushes trees and brush, while the blade chops the slash (c), resulting in a bed of crushed slash and distinct soil disturbance patterns (d). Hydro-axing involves using a tractor with an articulating mulcher-head attached to the front that mulches stems < 8 inches in diameter (e). This technique produces a bed of fine mulch (f). Photo credits: Garrett Stephens (machinery) and Travis Gallo (plots post-treatment).

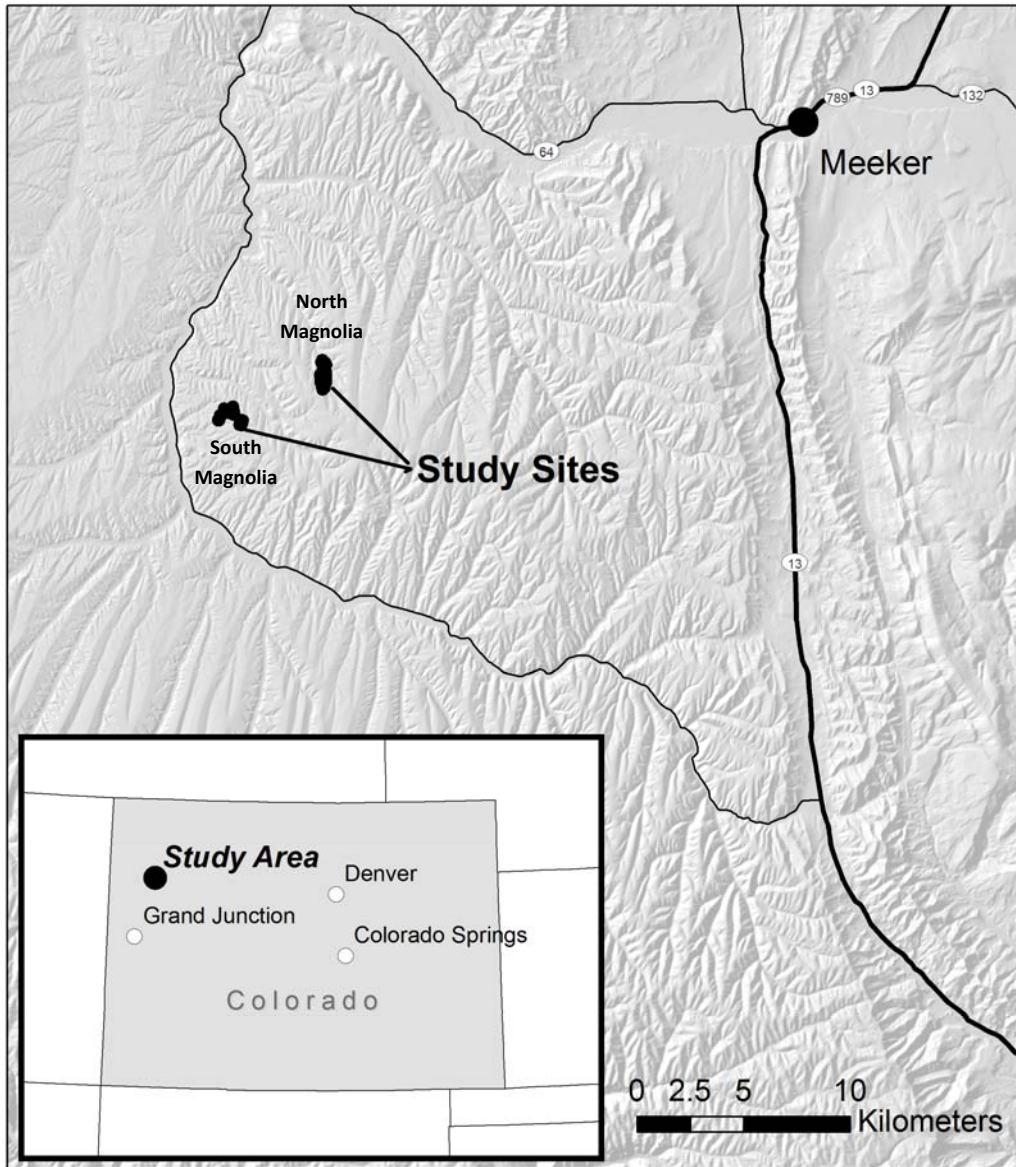


Fig. 2. Study site locations in the Piceance Basin, Colorado.

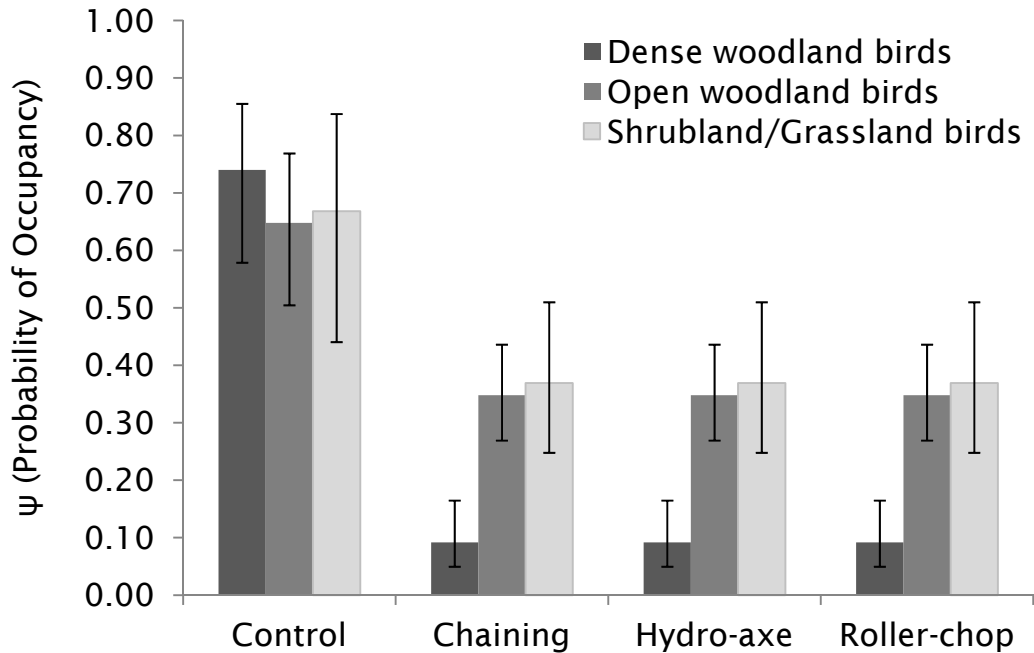


Fig. 3. Bird guild-based occupancy estimates from the top-ranked model in the bird habitat mitigation treatment model set, $\psi(\text{Control} \times \text{Habitat guild}) / p(\text{Control} + \text{Detection guild})$, model weight = 45%. Bars depict 95% confidence intervals.

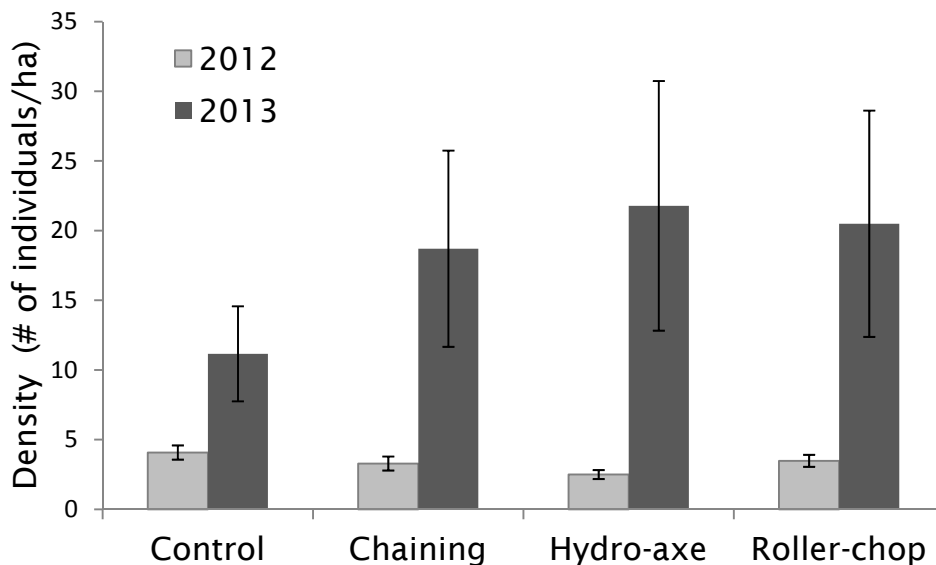


Fig. 4. Mean deer mouse density estimates for different experimental mule deer habitat mitigation treatment and control plots ($n = 7$ plots/treatment or control, 28 total) during 2012 and 2013 in the Piceance Basin, northwest Colorado. Estimates were calculated using Huggins closed-capture models and a variance components analysis to obtain derived mean estimates of abundance for each treatment. Abundance estimates were adjusted by plot area and probability of availability estimates to obtain mean density, corrected for availability. Bars depict 95% confidence intervals.

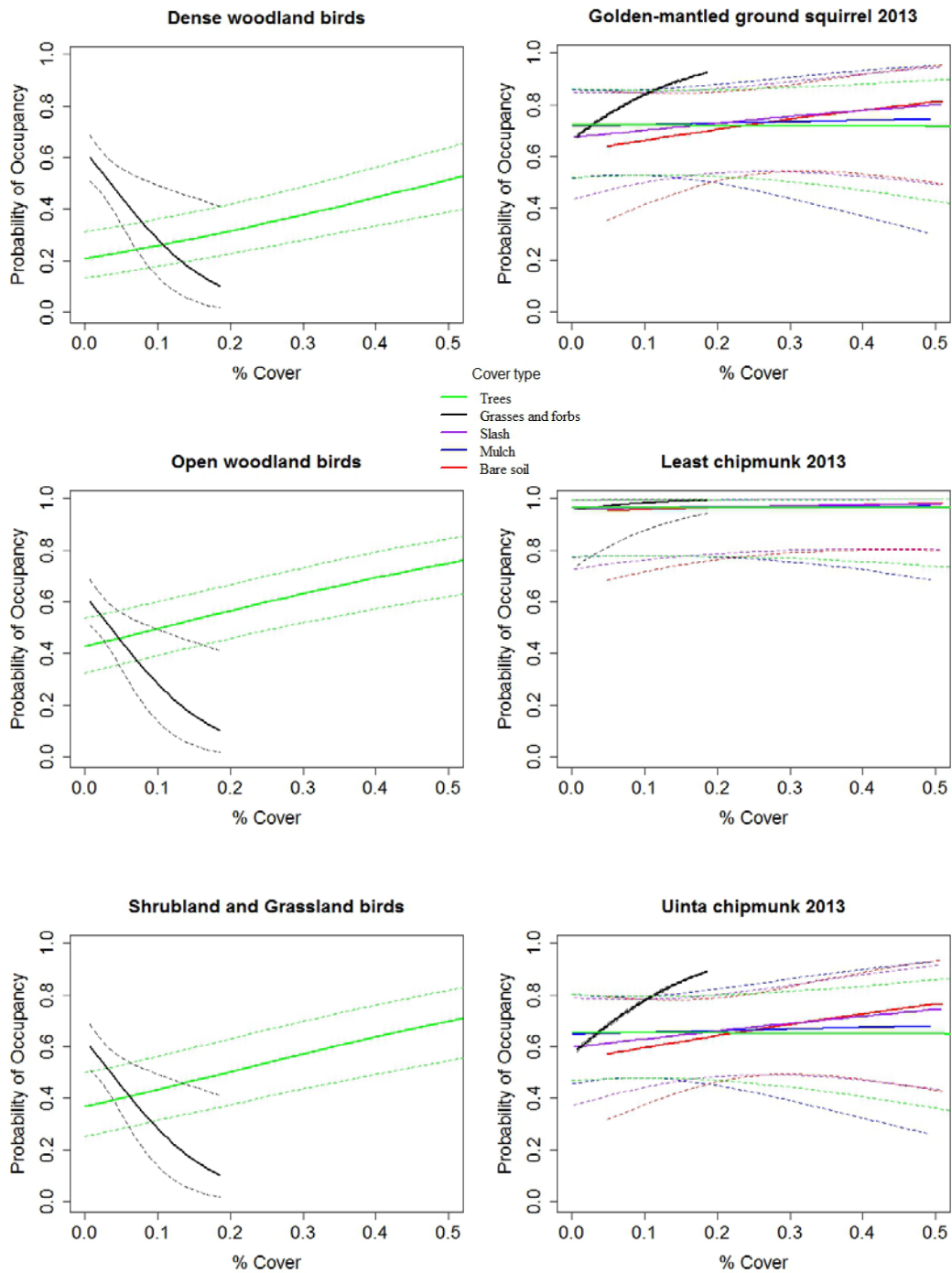


Fig. 5. Predicted bird guild or small mammal species occupancy values for a range of habitat characteristic cover values in different experimental mule deer habitat mitigation treatment and control plots ($n = 7$ plots/treatment or control, 28 total) in the Piceance Basin, northwest Colorado. Predicted values generated from separate multi-species occupancy analyses of each taxonomic group using estimates from the highest-ranking model in the model set containing the effect. Estimates depicted with solid lines and 95% confidence intervals depicted with dashed lines. Results for small mammal species were similar between 2012 and 2013, so only 2013 results are shown. Non-significant habitat characteristics from bird habitat models are excluded for clarity.

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APPENDICES

Appendix 1. Predictor variables included as covariates in bird single season site occupancy models and small mammal multiple season site occupancy models for experimental mule deer habitat mitigation treatment comparisons. Response variables modeled with specified predictor variables are indicated by ψ (probability of treatment site occupancy) or p_j (probability that species is detected in a treatment site in survey j). Taxonomic groups modeled with specified predictor variables are indicated by B (birds) and SM (small mammals). All possible combinations of models were run, and both additive and interactive effects of the “species” and “habitat guild” effects were run with each of the other occupancy covariates. *Models that included “Species” effects on both occupancy and detection did not converge and were excluded from the model set.

Predictor variable	Description (a priori hypotheses)	Response variables	Taxonomic groups
Treatment	Response variable varies by all treatments (control, chaining, hydro-axe, roller-chop)	Ψ, p_j	B, SM
Control	Response variable varies between control treatments and removal treatments only	Ψ, p_j	B, SM
Site	Response variable varies between the two separate sites in the study area	Ψ, p_j	B, SM
Habitat guild	Response variable varies by habitat guilds (dense woodland, open woodland, grassland/shrubland)	Ψ	B
Species*	Response variable varies by all species	Ψ, p_j	B, SM
Detection guild	Response variable varies by detection guilds (low, medium, and high detection based on additive index)	p_j	B, SM
Observer	Response variable varies by observer	p_j	B
Wind	Response variable varies by wind level	p_j	B
Cloud	Response variable varies by cloud level	p_j	B
Survey time	Response variable varies by time of survey	p_j	B
Year	Response variable varies by year	p_j	SM
Survey	Response variable varies by each survey occasion	p_j	SM
Constant	Response variable does not vary by measured variables	Ψ, p_j	B, SM

Appendix 2. Predictor variables included as covariates in bird single season occupancy models and small mammal multiple season occupancy models for habitat selection comparisons. Response variables modeled with specified predictor variables are indicated by ψ (probability of site occupancy) or p_j (probability that species is detected in a treatment site in survey j). Taxonomic groups modeled with specified predictor variables are indicated by B (birds) and SM (small mammals). All continuous variables were correlated between 2012 and 2013 for each effect ($p < 0.05$, Spearman's rank-order correlation), except grass and forb cover, so only values from 2012 were used in models for all variables except grass and forb cover. Shrub cover was positively correlated ($p < 0.05$, Spearman's rank-order correlation) with tree cover and was excluded from the model set. All possible combinations of models were run, and both additive and interactive effects of the "species" and "habitat guild" effects were run with each of the other occupancy covariates, when applicable. Models that included a site effect on occupancy and models that included species effects on both occupancy and detection did not converge and were excluded from the model set. * Effect modeled on detection for small mammals only (bird detection was only predicted to vary by tree cover, but not by shrub, grass and forb, slash, mulch or bare soil cover types).

Predictor variable	Description (a priori hypotheses)	Response variables	Taxonomic groups
Tree cover	Response variable varies by average % tree cover in plot	Ψ, p_j	B, SM
Shrub cover*	Response variable varies by average % shrub cover in plot	Ψ, p_j	B, SM
Grassforb cover*	Response variable varies by average % grass + forb cover in plot	Ψ, p_j	B, SM
Wood/slash cover*	Response variable varies by average % wood/slash cover in plot	Ψ, p_j	B, SM
Mulch cover*	Response variable varies by average % mulch cover in plot	Ψ, p_j	B, SM
Bare soil cover*	Response variable varies by average % bare soil cover in plot	Ψ, p_j	B, SM
Site	Response variable varies between the two sites in the study area	p_j	B, SM
Habitat guild	Response variable varies by habitat guilds (dense woodland, open woodland, grassland/shrubland)	Ψ	B
Species	Response variable varies by all species	Ψ, p_j	B, SM
Detection guild	Response variable varies by detection guilds (Birds: low, medium, and high detection based on additive index of detection characteristics [minimum body length, foraging habit, vocalization pitch, vocalization length, flocking habit, regional commonness]; Small mammals: nocturnal or diurnal species)	p_j	B, SM
Observer	Response variable varies by observer	p_j	B
Wind	Response variable varies by wind level	p_j	B
Cloud	Response variable varies by cloud level	p_j	B
Survey time	Response variable varies by time of survey	p_j	B
Year	Response variable varies by year	p_j	SM
Survey	Response variable varies by each survey occasion	p_j	SM
Constant	Response variable does not vary by measured variables	Ψ, p_j	B, SM

Appendix 3. Bird species encountered in the mule deer habitat mitigation treatment plots. *Species not included in occupancy models due to sparse data. **Data from Empidonax flycatchers were pooled and modeled as Empidonax spp. due to uncertainty in field identification of individual Empidonax species.

Cooper's hawk*	<i>Accipiter cooperii</i>
Mourning dove	<i>Zenaida macroura</i>
Common nighthawk*	<i>Chordeiles minor</i>
Black-chinned hummingbird	<i>Archilochus alexandri</i>
Broad-tailed hummingbird	<i>Selasphorus platycercus</i>
Williamson's sapsucker*	<i>Sphyrapicus thyroideus</i>
Downy woodpecker*	<i>Picoides pubescens</i>
Hairy woodpecker	<i>Picoides villosus</i>
Northern flicker	<i>Colaptes auratus</i>
Western wood-peewee*	<i>Contopus sordidulus</i>
Ash-throated flycatcher	<i>Myiarchus cinerascens</i>
Gray flycatcher**	<i>Empidonax wrightii</i>
Dusky flycatcher**	<i>Empidonax oberholseri</i>
Plumbeous vireo	<i>Vireo plumbeus</i>
Western scrub-jay	<i>Aphelocoma californica</i>
Clark's nutcracker*	<i>Nucifraga columbiana</i>
Common raven*	<i>Corvus corax</i>
Violet-green swallow	<i>Tachycineta thalassina</i>
Mountain chickadee	<i>Poecile gambeli</i>
Juniper titmouse	<i>Baeolophus griseus</i>
Bushtit*	<i>Psaltriparus minimus</i>
White-breasted nuthatch	<i>Sitta carolinensis</i>
House wren*	<i>Troglodytes aedon</i>
Blue-gray gnatcatcher	<i>Poliophtila caerulea</i>
Western bluebird*	<i>Sialia mexicana</i>
Mountain bluebird	<i>Sialia currucoides</i>
Hermit thrush*	<i>Catharus guttatus</i>
American Robin*	<i>Turdus migratorius</i>
Yellow-rumped warbler*	<i>Setophaga coronata</i>
Black-throated gray warbler	<i>Setophaga nigrescens</i>
Western tanager*	<i>Piranga ludoviciana</i>
Green-tailed towhee*	<i>Pipilo chlorurus</i>
Spotted Towhee	<i>Pipilo maculatus</i>
Chipping sparrow	<i>Spizella passerine</i>
Dark-eyed junco	<i>Junco hyemalis</i>
Brown-headed cowbird*	<i>Molothrus ater</i>
Cassin's finch	<i>Haemorhous cassinii</i>
Red crossbill	<i>Loxia curvirostra</i>
Evening grosbeak	<i>Coccothraustes vespertinus</i>

Appendix 4. Small mammal species encountered in the mule deer habitat mitigation treatment plots. *Species not included in occupancy or Huggins closed capture models due to sparse data.

Deer mouse	<i>Peromyscus maniculatus</i>
Least chipmunk	<i>Tamias minimus</i>
Uinta chipmunk	<i>Tamias umbrinus</i>
Golden-manteled ground squirrel	<i>Spermophilus lateralis</i>
Bushy-tailed woodrat*	<i>Neotoma cinerea</i>

Appendix 5. AIC model selection results for bird and small mammal habitat mitigation treatment occupancy models and habitat selection occupancy models. Modeled effects related to bird or small mammal occupancy (ψ) and detection (p) include: parameter varies by all habitat treatments (Treatment), by controls vs. treatments (Control), by habitat-based guilds for bird models only (Habitat Guild), by species (Species), by detection-based guilds (Detection Guild), by year of sampling for small mammal models only (Year), by survey occasion for small mammals only (Survey), by % cover of grasses and forbs in 2012 and 2013 (Grassforb2012 and Grassforb2013), by % cover of trees (Trees), by % cover of bare soil (Baresoil), by % cover of slash (Slash), or by % cover of mulch (Mulch). Models with $\Delta AICc$ values ≤ 7 are shown. Models with $\Delta AICc$ values ≤ 2 are all plausible best fitting models for the observed data, models with $\Delta AICc$ values >7 have little support (Burnham and Anderson 2002). K = # of parameters. *Bird habitat mitigation treatment models were adjusted by an overdispersion parameter ($\hat{c} = 2.28$), producing QAICc values. No overdispersion adjustment was needed for bird habitat selection models ($\hat{c} = 0.92$). Goodness-of-fit tests are not available for multiple season occupancy models (small mammals).

Model	K	AICc	$\Delta AICc$	AIC weight	Deviance
<i>Bird Habitat Mitigation Occupancy Models*</i>					
$\psi(\text{Control} * \text{Habitat Guild})p(\text{Control} + \text{Detection Guild})$	10	1188.52	0.00	0.45	787.51
$\psi(\text{Control} + \text{Habitat Guild})p(\text{Control} + \text{Detection Guild})$	8	1190.72	2.20	0.15	793.84
$\psi(\text{Control} * \text{Habitat Guild})p(\text{Treatment} + \text{Detection Guild})$	12	1191.47	2.95	0.10	786.30
$\psi(\text{Control} + \text{Species})p(\text{Control} + \text{Detection Guild})$	27	1191.58	3.05	0.10	754.36
$\psi(\text{Control})p(\text{Control} + \text{Detection Guild})$	6	1192.53	4.00	0.06	799.74
$\psi(\text{Treatment} + \text{Habitat Guild})p(\text{Control} + \text{Detection Guild})$	10	1193.53	5.01	0.04	792.52
$\psi(\text{Control} + \text{Habitat Guild})p(\text{Treatment} + \text{Detection Guild})$	10	1193.67	5.14	0.03	792.65
$\psi(\text{Treatment} + \text{Species})p(\text{Control} + \text{Detection Guild})$	29	1194.22	5.70	0.03	752.60
$\psi(\text{Treatment})p(\text{Control} + \text{Detection Guild})$	8	1195.31	6.79	0.01	798.42
$\psi(\text{Control})p(\text{Treatment} + \text{Detection Guild})$	8	1195.44	6.91	0.01	798.55
<i>Small Mammal Habitat Mitigation Occupancy Models</i>					
$\psi(\text{Species} + \text{Year})\epsilon(.)p(\text{Species} + \text{Year})$	9	750.79	0.00	0.48	731.65
$\psi(\text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	8	751.94	1.15	0.27	735.04
$\psi(\text{Control} + \text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	9	752.71	1.92	0.18	733.57
$\psi(\text{Treatment} + \text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	11	755.56	4.77	0.04	731.87
<i>Bird Habitat Selection Occupancy Models</i>					
$\psi(\text{Trees} + \text{Habitat Guild})p(\text{Trees} + \text{Species})$	27	2664.18	0.00	0.71	2607.61
$\psi(\text{Trees} + \text{Species})p(\text{Trees} + \text{Detection Guild})$	27	2666.22	2.04	0.26	2609.65
$\psi(\text{Trees})p(\text{Trees} + \text{Species})$	25	2671.12	6.94	0.02	2618.91
<i>Small Mammal Habitat Selection Occupancy Models</i>					
$\psi(\text{Site} + \text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	9	750.73	0.00	0.29	731.59
$\psi(\text{Grassforb2013} + \text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	9	751.35	0.62	0.21	732.21
$\psi(\text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	8	751.94	1.22	0.16	735.04
$\psi(\text{Baresoil} + \text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	9	753.42	2.69	0.07	734.28
$\psi(\text{Slash} + \text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	9	753.56	2.83	0.07	734.42
$\psi(\text{Grassforb2012} + \text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	9	754.01	3.28	0.06	734.87
$\psi(\text{Mulch} + \text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	9	754.16	3.43	0.05	735.02
$\psi(\text{Trees} + \text{Species})\epsilon(.)p(\text{Species} + \text{Year})$	9	754.18	3.45	0.05	735.04

Appendix 6. Total # of individuals captured for small mammals found in experimental mule deer habitat mitigation treatment and control plots (n = 7 plots/treatment or control, 28 total) in the Piceance Basin, northwest Colorado. Small mammal data were collected during June-July 2012 and July 2013.

Species	Total # of individuals captured							
	2012				2013			
	Control	Chain	Hydro -axe	Roller -chop	Control	Chain	Hydro -axe	Roller- chop
Deer mouse	72	58	47	57	203	297	340	314
Least chipmunk	28	67	20	49	19	25	27	23
Uinta chipmunk	10	11	1	10	8	8	6	5
Golden-mantled ground squirrel	5	12	18	19	3	2	2	2
Bushy-tailed woodrat	0	0	0	0	3	1	0	0
Totals	115	148	86	125	236	333	375	344